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A STUDY OF TERRITORY ESTABLISHMENT BY AND MOVEMENTS OF MALE SHARP-TAILED GROUSE (*PEDIOECETES PHASIANELLUS*) RELATIVE TO THE ARENA

by

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A THESIS

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The undersigned certify that they have read, and recommend for acceptance, a thesis entitled "A study of territory establishment by and movements of male sharp-tailed grouse (*Pedioecetes phasianellus*) relative to the arena" submitted by David L.J. Moyles in partial fulfilment of the requirements for the degree of Master of Science.

"To live is to dance; to dance is to live."
-- Charles Schultz

"Dance then where ever you may be; I am the Lord of the Dance, said he;"
--Sydney Carter

ABSTRACT

The manner in which young male sharp-tailed grouse established new territories on arenas near Wainwright, Alberta, was observed during autumn, winter and spring of 1975 and 1976. Males established territories at the peripheries of arenas where they seemed to require two to five display sessions to integrate with the lekking cohort. Persistent efforts by a given male, concentrating its activities on the edge of the arena, appeared to be important to its success in acquiring a territory. This process may have required recognition by resident territorial male(s) as well as a position in a dominance hierarchy. Most males took territories during autumn and winter; adult males (probably birds entering their second winter) were more successful in establishing territories in autumn than were juvenile males (entering their first winter).

The movements of lekking and non-lekking males were determined off the arena. Resident and newly-established territorial males showed an affinity for areas immediately around the arena. Ranges of these males around an arena were usually discrete from those of other arenas. There were two groups of non-territorial males, based on their movements relative to the capture arena. The grouse in one group stayed near the arena and appeared to restrict their

attempts to establish territories to that arena. Grouse in the other group moved away from the arena of capture, possibly seeking other arenas on which to establish themselves.

I discuss the role of non-territorial males in the formation and maintenance of arenas.

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INTRODUCTION

Evidence indicates that, for several species of tetraonids, some males are excluded, probably annually, from the breeding population (Watson and Jenkins 1967; Robel 1969; Fischer and Keith 1974; Rippin and Boag 1974a). Such males may group together into a non-breeding cohort (Robel 1969) or remain dispersed (Herzog 1977); their fate remains largely unknown. Descriptive and experimental studies have centered on the breeding cohort of tetraonid populations, probably because of the conspicuousness of breeding grouse during spring display (Hjorth 1970) and the fact that when breeding they all become territorial and hence spatially sedentary; the non-breeding cohort has remained largely unstudied. Robel (1969) stated that 60 % of male black grouse (*Lyrurus tetrix*) were non-lekking, mainly yearling males. Rippin and Boag (1974a) showed that the number of non-lekking male sharp-tailed grouse (*Pedioecetes phasianellus*) available for recruitment onto arenas in March was approximately equal to the number of lekking males. They believed the majority of these birds were also yearlings. Thus, non-lekking males can comprise a significant segment of the male population in these two species.

Little is known about either the timing of entry of males into the lekking cohort, the age of the males involved, or the position on the arena initially occupied by

newly recruited males. Hamerstrom and Hamerstrom (1951) reported that juvenile male sharptails displayed with adult males in autumn. Both Brown (1970) and Rippin (1970) recorded juvenile males present on arenas during autumn displays. Rippin and Boag (1974a) showed, through removal experiments, that recruitment onto arenas during March was rapid. That they recorded no recruitment during April, May and June may have indicated that lekking male sharptails located peripherally on arenas determined the rate of recruitment of non-territorial males (Rippin and Boag 1974a,b).

Movements of non-territorial male sharp-tailed grouse, relative to the arena, are not known. Hamerstrom and Hamerstrom (1951) recorded the basic pattern of movements throughout the year in Wisconsin but did not distinguish between lekking and non-lekking males.

Several questions concerning the movements and recruitment of male sharp-tailed grouse into the lekking cohort remain unanswered. When, and at what age, does a male gain a territory on an arena? Do all non-territorial males gain territroy, and if not, why do some not gain territory? Where do males establish their first territories on arenas - on the periphery or towards the center? Are non-lekking males associated with one arena only or do they behave as non-lekking blackgrouse and wander from arena to arena (Johnstone 1969)? Are these non-territorial male sharp-tailed grouse "surplus" in the sense that they are not

important to the general biology of the sharp-tailed grouse?

The objectives of this study were to determine the timing of entry and position taken by male sharp-tailed grouse establishing themselves in a group of lekking males and to compare movements of the non-lekking males with those of lekking males. By answering these questions, I hoped to determine the significance of non-territorial males in the population dynamics of this species.

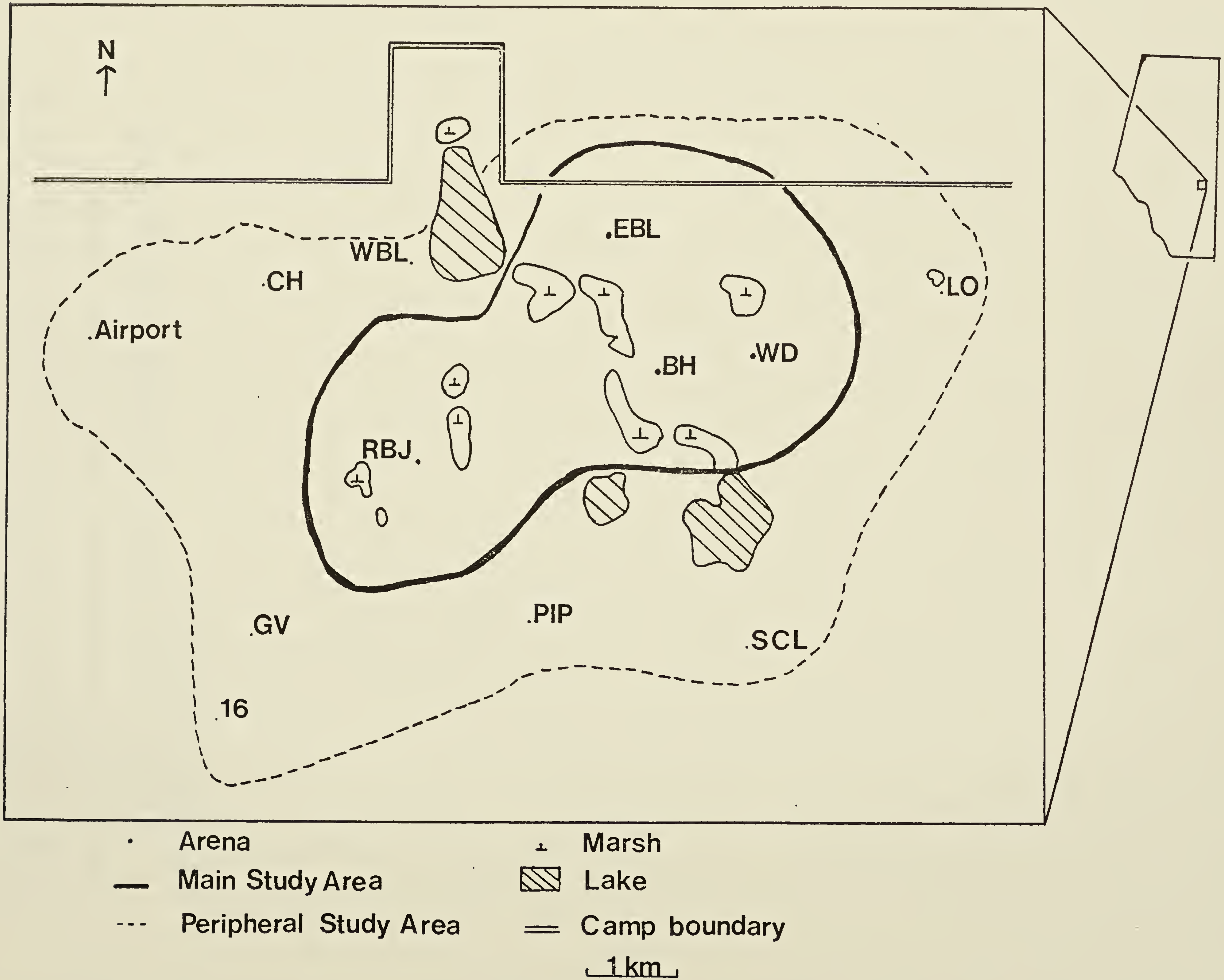
STUDY AREA

This study was conducted on the Camp Wainwright Military Reserve, a detachment of Canadian Forces Base Calgary (Fig. 1). The main study area encompassed approximately 28 sq km within which four arenas were located. Copses of trees and grasslands covered approximately 54 and 46 % of the area, respectively, with less than 1 % in marshland. A peripheral study area encompassed the habitat immediately outside the main study area and included an additional eight arenas.

The northern half of the main study area had not been burned for several years and consequently the aspen (*Populus tremuloides*) community was encroaching on the grassland community (Appendix 1). In these aspen copses some trees reached 10 m in height. Shrubs, such as *Prunus virginiana*, *Amelanchier alnifolia*, *Elaeagnus commutata*, *Rosa* spp., *Symphoricarpos albus* and *S. occidentalis* tended to be concentrated in the transition zone between the trees and the grassland where moisture and terrain conditions favoured their growth. The grasslands were dominated by *Bouteloua gracilis*, *Bromus inermis*, *Festuca* spp., and *Stipa* spp. *Salix* spp. and *Carex* spp. dominated the marsh area.

Military activity affected the area in two ways. Military personnel periodically burned sections of the camp to decrease the probability of wildfire. The main and peripheral study areas have been burned very irregularly

Figure 1. Study area in Camp Wainwright Military Reserve, Alberta.


N
WBL
.EBL
.CH
.LO
.Airport
.BH
.WD
RBJ.
.PIP
.GV
.SCL
.16
Arena
Main Study Area
Peripheral Study Area
Marsh
Lake
Camp boundary
1 km

over the last 8 years (Appendix 1). The army also made extensive use of all-terrain and tracked vehicles which created trails and openings through aspen clumps.

Limited grazing occurred throughout the main and peripheral study areas.

METHODS

Capture, marking and observation on arenas

In order to meet the objectives of this study, I had to know the age and identity of all male sharp-tailed grouse seen on arenas as well as the position of territories held by all lekking males.

Territorial and non-territorial males were trapped on the four arenas of the main study area during spring, autumn and winter of both 1975 and 1976. Walk-in traps and mist nets, as described by Rippin (1970) and Evans (1961), respectively, were used to capture males. A drop net also was used to capture grouse on arenas (Appendix 2). Noose carpets (Anderson and Hamerstrom 1967) were used to capture grouse during spring and autumn displays in 1976.

Each grouse captured in the main study area was banded with one numbered aluminum band and three coloured plastic 'Darvic' bands in a unique combination so that capture arena, sex, and identity of each banded grouse could be determined. Most of the males were tagged with coloured patagial streamers (Rippin 1970). The coloured streamers were specific for each arena and identified the sex and territorial status of each grouse: territorial males, non-territorial males and females.

Sex of each grouse captured was determined by checking the crown feathers and central rectrices (Henderson *et al.* 1967, Snyder 1935). Age was determined by measuring the

diameter, at the superior umbilicus, and length of the proximal (first) primary (Wishart et al. 1976).

Territorial males on arenas in the peripheral study area were captured in spring of both 1975 and 1976. Each male was banded with one numbered aluminum band and one coloured plastic 'Darvic' band to identify the arena on which it had been captured. Most of these males also were marked with patagial wing tags, a different colour identifying each arena.

Arenas on the main study area were mowed to facilitate reading leg bands and gridded with a fan-shaped pattern of stakes radiating out from a fccal point 1 m in front of the blind (Rippin 1970). The territorial boundaries of lekking males could be determined by plotting the 'face-offs' (Lumsden 1965), relative to the grid system, between neighbouring males.

Sounds of displaying territorial males, recorded at Arena WD, were replayed at Arenas EBL, RBJ and WD in an attempt to attract males back to the arena after flushing. Reactions of territorial males to the calls are shown in Appendix 3.

Morning displays in spring, autumn and winter of both 1975 and 1976 were observed and interactions between territorial and non-territorial males as well as among territorial males were recorded. The number of females observed on each arena during each session was recorded. As the number of marked females was low, each female sighted

was recorded as one female-visit. For comparative purposes, the total number of female-visits to each arena was divided by the number of displays observed.

Movement

Telemetry gear was used to determine the locations of males off the arena. Both territorial and non-territorial males were equipped with radio transmitters in autumn 1975 and winter, spring and autumn of 1976. In autumn, 1975, transmitters supplied by S.M. Markusen, Electronics Specialties, Esko, Minnesota were used. In 1976, in addition to the Markusen units, transmitters supplied by AVM Instrument Company, Champaign, Illinois were used. Transmitters emitted constantly pulsing signals in the frequency range of 150.815 to 151.150 MHz. Mallory RM1 mercury batteries were used to power the units. Each male was outfitted with a 'backpack' similar to units used by Herzog (1977) except that a heavier, stronger harness cable was used. Weights of transmitters ranged from 24 to 29 g; all units were less than 4 % of the body weight of the grouse.

Positions of radio-tagged grouse were determined by two methods. Grouse were located with a hand-held 4-element yagi antenna attached to a receiver. The tracker walked towards the area from which the signal was coming, eventually flushing the grouse. The second method involved triangulation. Bearings to the transmitter-tagged grouse were taken simultaneously at two antenna towers. Each tower was equipped with an 11-element directional yagi antenna mounted on top of a 7-m mast supported by a metal tripod and a base plate. A compass dial was mounted on top of the base

plate. By plotting bearings on a large scale aerial photograph (1mm=8m), locations could be determined. Accuracy of the triangulation method was tested in summer and winter (Appendix 4).

Habitat use

The location of each grouse was determined before flushing, if possible. If not, the flush point of the grouse was considered to be its location. Only in summer was it difficult to see the grouse before they flushed.

The vegetation within a 1-m radius around each grouse or the flushing point was classified into one of seven vegetation classes:

1) grassland - dominated by grasses and forbs,

2) grassland-low shrub transition - a mixture of grasses, forbs, and woody shrubs less than 1 m in height,

3) low shrub - dominated by woody shrubs less than 1 m in height,

4) low shrub-tall shrub transition - a mixture of low shrubs and tall shrubs greater than 1 m but less than 3 m in height,

5) tall shrub - dominated by woody shrubs greater than 1 m but less than 3 m in height,

6) trees - dominated by woody vegetation greater than 3 m in height,

7) marsh - dominated by _Carex_ spp. and _Salix_ spp.

All observers practised classifying vegetation until classifications were consistent between observers.

A 1 sq m plot was placed around grouse locations in grassland, grassland-low shrub transition, low shrub and marsh vegetation types while a 3 sq m plot was used for grouse locations in low shrub-tall shrub transition, tall shrub or tree vegetation types. Coverage of all species present within the plot was recorded. Six coverage classes, described by Daubenmire (1968), were used. Moss (1967) was followed for identification and taxonomy of vascular plants.

Upon location of one or more transmitter-tagged males, the total in the group and number marked were recorded. The colour of all wing tags observed also was recorded. Weather conditions, such as wind speed, temperature, cloud cover, and presence or absence of moisture on the vegetation were noted. The area around each sighting was thoroughly searched with trained dogs to ascertain that all grouse near the radio-tagged individuals had been seen.

During the summers and winters of 1975 and 1976, the areas within 1200 m of the arenas on the main study area were censused systematically with trained pointing and flushing dogs. The same procedure as detailed for recording of location, weather conditions and vegetation for all sighting of transmitter-tagged grouse was followed for sightings of all sharp-tailed grouse. Locations of marked grouse were plotted on a large-scale aerial photograph to determine distance of the grouse from the capture arena.

I wanted to determine the 'area of origin' of juvenile sharp-tailed grouse appearing on arenas during autumn

display. Broods were located with trained pointing dogs and chicks were captured by hand or by flushing them into a mist net. They were tagged with numbered metal patagial tags and coloured patagial streamers (Boag *et al.* 1975). Four walk-in traps with leads (Liscinsky and Bailey 1955) were set in the main study area in summer, 1975. Each trap was baited with barley and checked twice daily.

Analysis of movements

Distances from the capture arena to locations of all males sighted were determined from a grid system consisting of squares 10 cm by 10 cm superimposed on the large scale aerial photograph. Mean locations were determined by averaging all locations. Home ranges were determined using the modified minimum home range method described by Harvey and Barbour (1965) as modified by Herzog (1977). Each square of the grid was subdivided into 100 squares 1 cm by 1 cm. The minimum daily movement for all transmitter-tagged males was determined by counting the number of 1 cm squares through which a male grouse moved in 1 day. The number of squares between consecutive locations was determined by drawing a straight line between the points and counting all squares touched by the line. Mean daily movement was determined by averaging the number of squares moved each day.

Each 10-cm square of the grid system was subdivided into four squares 5 cm by 5 cm and superimposed over the movements of radio-tagged males. A straight line was drawn

between points and a square was considered used by a male if the line touched any portion of the square. Each square used was counted only once. The cumulative number of squares used by each male was plotted as a function of the number of sightings. The slope for each plotted line was determined as an indication of the degree of affinity with one area; a 'steep' slope indicating little affinity while a 'shallow' slope indicated affinity with an area.

Statistical tests used in the analysis of data were taken from Nie *et al*. (1975), Siegal (1956), and Sokal and Rohlf (1969). The 5 % level of probability was used as the level of significance in all tests.

RESULTS AND DISCUSSION

Recruitment

A male sharp-tailed grouse must defend a territory on an arena in order to be part of the potential breeding population (Evans 1961; Johnsgard 1973). The potential 'recruit' must overcome aggressive responses of established territorial males before acquiring a territory.

The general pattern of acquisition was similar in 29 of 32 cases observed (Table 1). The acquisition of a territory seemed to take three to five display sessions to complete. Non-territorial males appeared to watch displaying males either from the periphery of the arena or from a vantage point such as a tree, a trap or the top of the drop net. These vantage points allowed the males to watch the display without being attacked by the territorial males. Some non-territorial males walked onto the arena with crest feathers erect but most walked onto the arena with feathers sleeked to their bodies. A non-territorial male would try to remain in a small area on the arena, usually at the periphery where initially it remained crouched. After one or two display periods, the male establishing itself would display to and drive off non-territorial males in a manner similar to that of territorial males displaying to one another. At this time the male gaining a territory would walk from advancing territorial males, in contrast to non-territorial males which ran from an advancing male. The male was considered

Table 1. Number, age and location at which newly-recruited male sharp-tailed grouse established territories throughout the year.

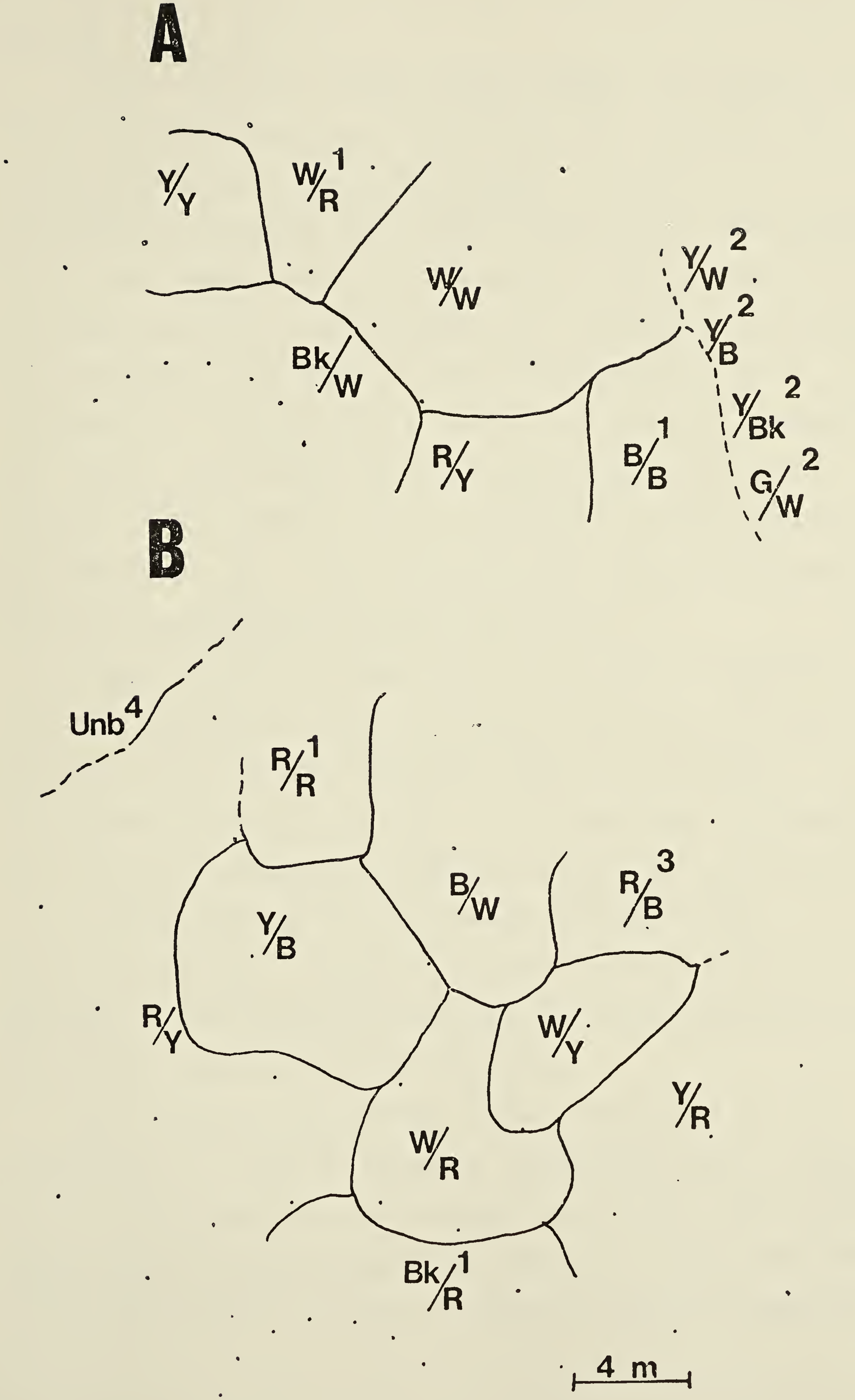
Arena	Number of males	Age		Position of territory			Time of acquisition	
		Ad	Juv	Central	Peripheral	Unknown	Sept.- Apr.	Apr.- June 15
BH	4	0	4	0	4	0	4	0
EBL	4	0	4	0	4	0	4	0
RBJ	16	11	5	0	11	5	15	1
WD	5	5	0	0	5	0	2	3

to have established a territory when it could maintain boundaries with the other territorial males.

New territories were established on the periphery of arenas (Table 1, Fig. 2). In three cases non-territorial males attempted to gain centrally-located territories after they had been vacated by their previous occupant. In all cases the neighbouring territorial males displayed to and fought with the new male for that entire display session. In two cases, the new birds did not return during subsequent display periods. In the third, the new bird did return and held the territory until the previous occupant, absent from the arena for 6 days after being fitted with a transmitter, returned and evicted the new bird after a period of 4 days.

Non-territorial males seemed to concentrate their attempts to gain territory in specific parts of an arena. On seven occasions, marked males appeared and tried to display in areas where they had been previously seen or caught. Such activity may aid them in acquiring a territory. By appearing continually on one part of the arena, the male could occupy territory in that area quickly should the resident territorial male not appear for display. A non-territorial male may become recognized by the nearest resident male by being persistent in its attempts to gain territory at a given point. Although initial encounters are usually brief, non-territorial males do try and display towards the lekking male during successive encounters. Eventually a male does establish itself as did male R/R on

Figure 2. Territories of male sharp-tailed grouse recorded in autumn on Arena BH (A) and EBL (B). Dots indicate the grid system on the arena (see text).
1 Territories of newly established males.
2 These four males attempted unsuccessfully to gain territory behind the dotted line.
3 This male was in the process of gaining territory but was killed away from the arena.
4 An unbanded male displayed for two sessions but was not seen again.


A
Y/Y
W/R 1
W/W
Bk/W
R/Y
B/B 1
Y/W 2
Y/B 2
Y/Bk 2
G/W 2
B
Unb 4
R/R 1
B/W
R/B 3
Y/B
R/Y
W/Y
Y/R
W/R
Bk/R 1
4 m

arena EBL (Fig. 2).

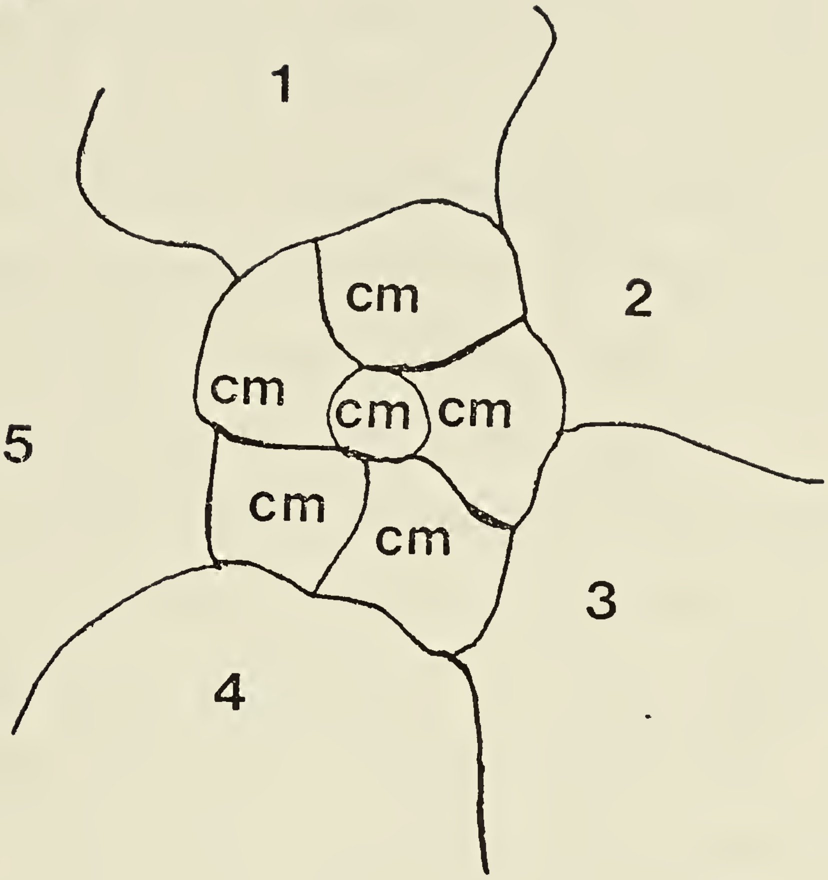
Rippin and Boag (1974b) did not record recruitment on the two experimental arenas from which they sequentially removed the central territorial males. Perhaps the peripheral territorial males had enlarged their territories towards the center while retaining all of their former territory (Fig. 3). The attempts of a non-territorial male concentrating in one spot to gain territory may place 'pressure' on a lekking male to move inwards when possible. The central territories seem to be preferred territories (Rippin and Boag 1974b) but the peripheral males still may have defended their former space as there was no 'pressure' on them to concentrate towards the center.

Rippin and Boag (1974b) postulated that a dominance hierarchy existed in groups of territorial males with the distance of a territory from the center of the arena determining position of a male in the hierarchy. Peripheral males may be redirecting aggressive attacks from the central males towards more peripheral non-territorial males. Without territory, a non-territorial male would not have a position in the dominance hierarchy and would presumably be relatively easy to drive off the arena.

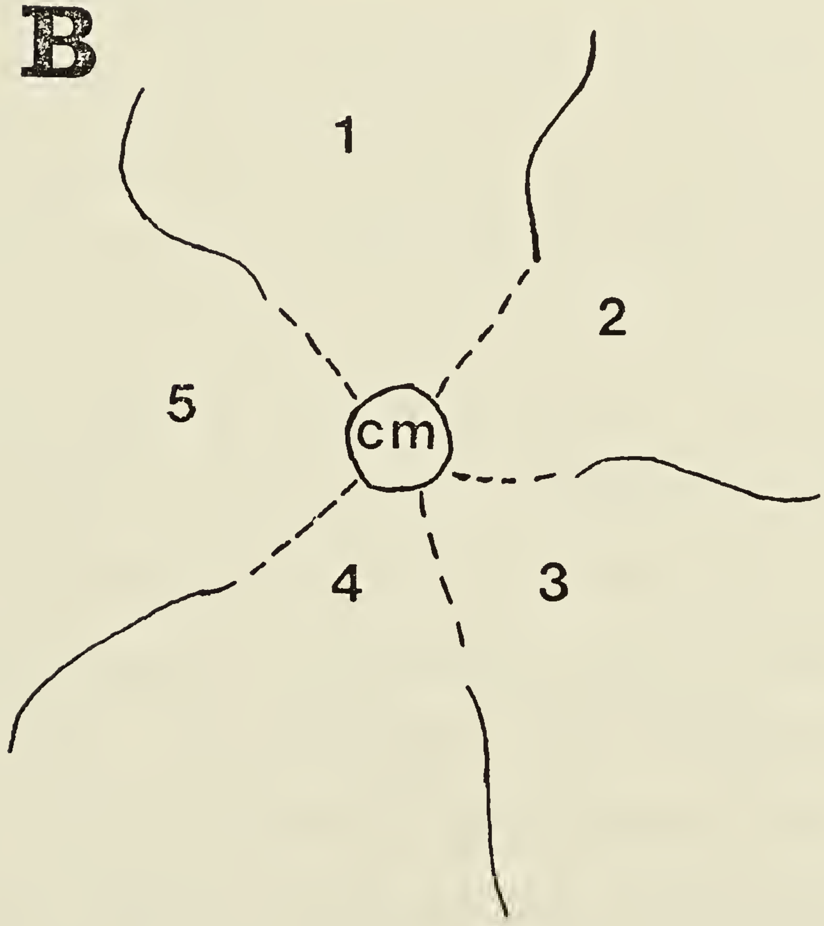
In a dominance hierarchy, mutual recognition by all members of the group is essential (Armstrong 1965). Rippin (1970) postulated that neighbouring territorial male sharp-tailed grouse could recognize one another since he was able to use differences in colour of feather tracts to identify

Figure 3. A sharp-tailed grouse arena showing a hypothetical arrangement of six centrally-located territorial males (cm) and five peripherally-located males (1-5) before (A) and after (B) removal of five of the central males. Dotted line in B separates newly acquired territory which may have been added to space formerly held (separated by solid lines).

A



B



individual males on an arena. Hamerstrom and Hamerstrom (1973) also used differences in facial, throat, and undertail feather patterns to identify individual lekking male greater prairie chickens (Tympanuchus cupido). Kermott and Oring (1975) have demonstrated that the "gobble" call is unique for each territorial male sharp-tailed grouse on one arena. A combination of acoustical and visual characteristics may allow males to recognize one another. During the last phase of territory acquisition, the new male establishes and maintains boundaries with its neighbours and thereby could become recognized by its neighbours. Other territorial males could learn to recognize the new male during successive displays.

Acquisition of a peripheral territory may be accomplished only after the new male has entered into the dominance hierarchy and is recognized by other lekking males. Non-territorial males would not be recognized by lekking males and would be chased by them. The great amount of fighting seen when a new recruit occupies a recently-vacated central territory may be the result of the inability of the territorial males to recognize this new male and hence their attempts to establish their positions relative to the new bird. Males gaining territories on the periphery would not have the intense pressure from territorial males that are high on the dominance scale. The new peripheral male would have a low status on the arena but would be of equal status in relation to other peripheral males (Rippin

and Boag 1974b).

The timing of territorial acquisition is shown in Table 1. Twenty-five males, both adult and juvenile, gained territory during autumn and winter and four gained territory in spring. In autumn, established males moved centripetally into vacancies created by summer mortality (Table 2) and possibly attempted to hold enlarged territories. Non-territorial males established themselves as the longer boundaries appeared to have been too large to defend adequately. Vacancies also appeared during winter as lekking males disappeared from arenas (Table 2). Thus, a male established on the periphery in autumn or winter would have more opportunity to gain territory closer to the center by the following breeding season. For example, the physical location of male W/Y's territory did not change but its status on Arena RBJ increased from that of a peripheral male in autumn 1975 to that of one of the central males by spring 1976 (Fig. 4) by having other males recruited around it. Males establishing territories in autumn and winter would tend to move with the lekking males, thereby gaining from their familiarity with the area and demonstrated superior survival. Survival of the older grouse may be related to choice of secure roosting and feeding areas. Furthermore, feeding or roosting as part of a flock may be selectively advantageous in that potentially more grouse are watching for predators (Appendix 5). Although snow roosting is probably an innate response to temperature and snow

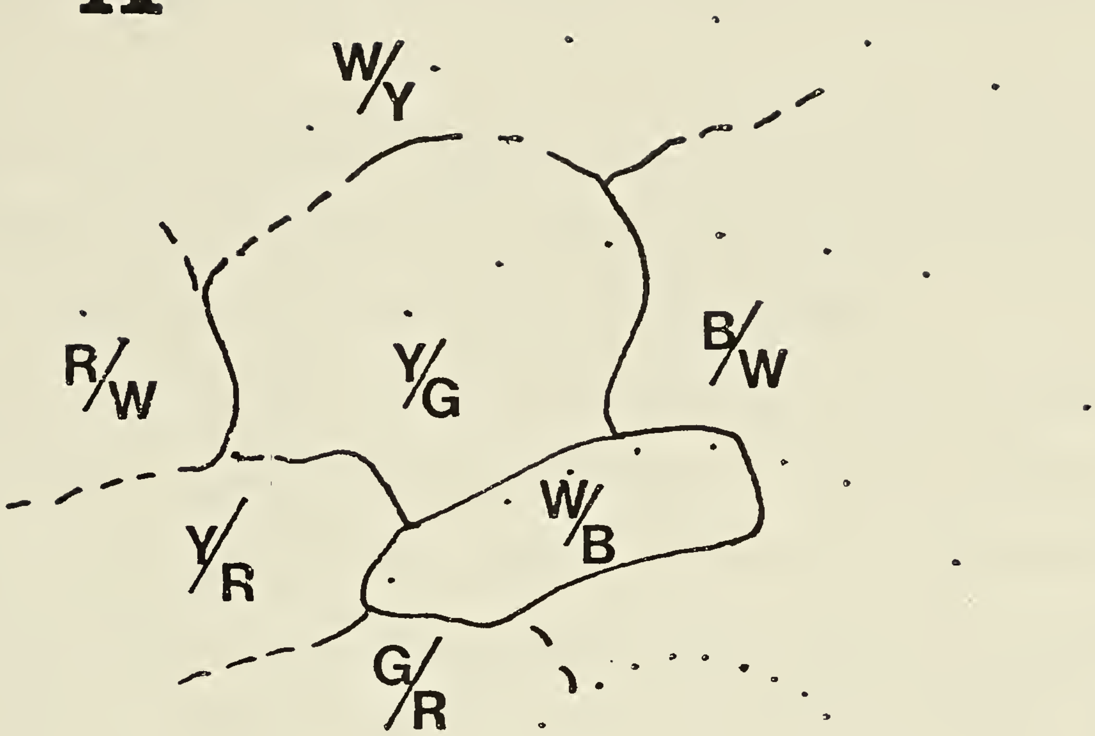
Table 2. Mortality among territorial male sharp-tailed grouse during the summer and winter seasons.

Arena	Number of Lekking Males					
	Present in spring		Returning in autumn		Newly-marked in autumn	Returning in spring
	Marked	Total	Marked	Total		
BH-1975	0	5	0	4 (80)[1]	4	1 (25)[2]
BH-1976	9	10	5	5 (50)	2	3 (43)
EBL	6	10	6	6 (60)	3	2 (22)
RBJ	6	13	4	4 (32)	4	2 (25)
WD	10	15	5	7 (47)		3 (43)
Airport	0	17	0	8 (47)		
CH	5	17	1	8 (47)		
LO-1975	7	24	1	11 (46)		
LO-1976	9	25	1	12 (48)		
M1	0	17	0	5 (29)		
WBL	0	4	0	0 (0)		

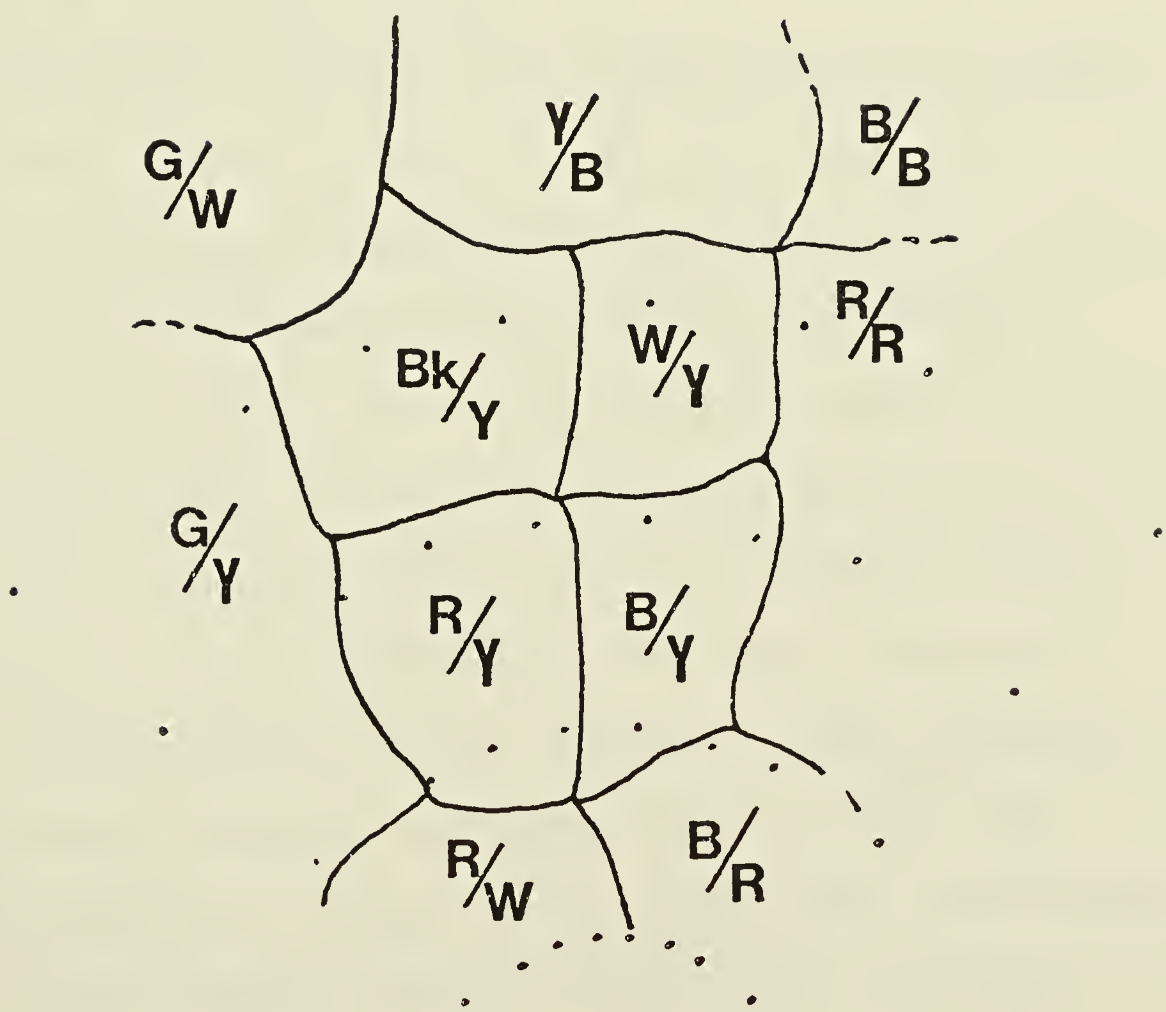
1 Percentage survival from spring to autumn
2 Percentage survival from autumn to apring

Figure 4. Territories of male sharp-tailed grouse of Arena RBJ in autumn 1975 (A) and spring 1976 (B). As a result of recruitment in winter, male W/Y became one of the central males.

A



B



conditions (Godfrey 1970), older males may be more aware of locations where snow concentrations are appropriate for roosting.

By spring the maximum number of territorial males on an arena had been established; new birds were recruited only when one of the territorial males disappeared.

Based on the number of non-territorial males caught and marked in autumn, the ratio of juvenile to adult males gaining territory was almost equal (Table 1). However the ratio of successful to unsuccessful adult males in autumn was significantly greater than that of juvenile males (Table 3). Adult males probably had a competitive advantage because of their previous experience in attempting to establish themselves on arenas. These birds were probably yearlings in their second autumn.

Weights of both territorial and non-territorial males captured during autumn displays of 1975 and 1976 were compared as a gross indication of general condition of the males. There was no significant difference in weight between previously established males (N=12), newly-established males (N=9) and non-territorial males (N=13) ($F=2.85; P>0.05$). However, adult territorial males (N=12) were significantly heavier then juvenile non-territorial males (N=11) (Mann-Whitney $U=119$; $P<0.05$). The difference in weights between juvenile terriorial males (N=9) and juvenile non-territorial males (N=11) approached statistical significance (Mann-Whitney $U=84$; $0.10>P>0.05$). A light

Table 3. Comparison of the rate of success of adult and juvenile male sharp-tailed grouse in establishing territories in autumn and winter.

Age	Fate	
	Success	Failure
Adult	13	2
Juvenile	12	12

G= 4.17; $P<0.05$

juvenile male sharp-tailed grouse may have been at a disadvantage in comparison to heavier juveniles and adult males. If weight of juvenile males approximated the growth curve described by Pepper (1972), then perhaps juveniles hatching in mid-July would have had less of a chance in their first attempt to gain territory than would juveniles hatched in early June. However, weight can only be considered a rough index to success in acquiring a territory as male R/R gained territory on Arena EBL in autumn 1975 yet only weighed 780 g in contrast to 854 g average weight of the adult territorial birds.

Some non-territorial males were observed to display to and chase other non-territorial males while on the edge of the arena. One non-territorial male would raise its crest, give the "gobble" call, walk and make pecking motions towards the other males. On all but one occasion, the other males ran from the aggressive one. In the one exception, the aggressive male and another male had a 'face-off' encounter similar to those between lekking males. These two males were not captured so their subsequent success or failure was not known. Perhaps the degree of aggressiveness of a male strongly influenced its chances of gaining territory.

In summary, males established territories initially on the periphery of arenas. Establishment involved localizing in one area and defending it firstly against other non-territorial males and ultimately against established , more

central males. This process appeared to require mutual recognition by the grouse involved. Frequencies of vacancies on arenas partially determined rate of recruitment but persistent efforts by non-territorial males in localized areas also were important for acquisition of territory. Although males were recruited into the lekking population from autumn to late spring, most established territories in autumn and winter. Adult males were more successful in acquiring territory in autumn than were juveniles. The general physiological condition of a male, especially a juvenile, appeared to be critical to its establishment on an arena.

Movements

Territorial males showed a marked affinity for the area around the arena (Fig. 5). It appeared that about 25 sightings were necessary to be relatively confident that the area used was maximal. This area varied from about 32 ha to 164 ha. The area used during spring and autumn and early winter remained relatively constant. The males made long flights from the arenas over this area from autumn to spring, averaging (with 95 % confidence limits) 9.1±2.6 and 8.3±2.8 squares daily in spring and in autumn and winter, respectively. Although there were only 11 sightings of wing-tagged territorial males in midwinter (Fig. 6), movements were probably similar to those of early winter and late winter. Rippin (1970) reported that 97 % of territorial males sighted in summer were seen within a

Figure 5. Total area used by eight marked territorial male sharp-tailed grouse from three arenas in spring, 1976. Each 'square' used encompassed 16 ha. Grouse numbered 1-3 were from Arena BH, grouse numbered 4-7 from Arena RBJ, and grouse number 8 from Arena WD.

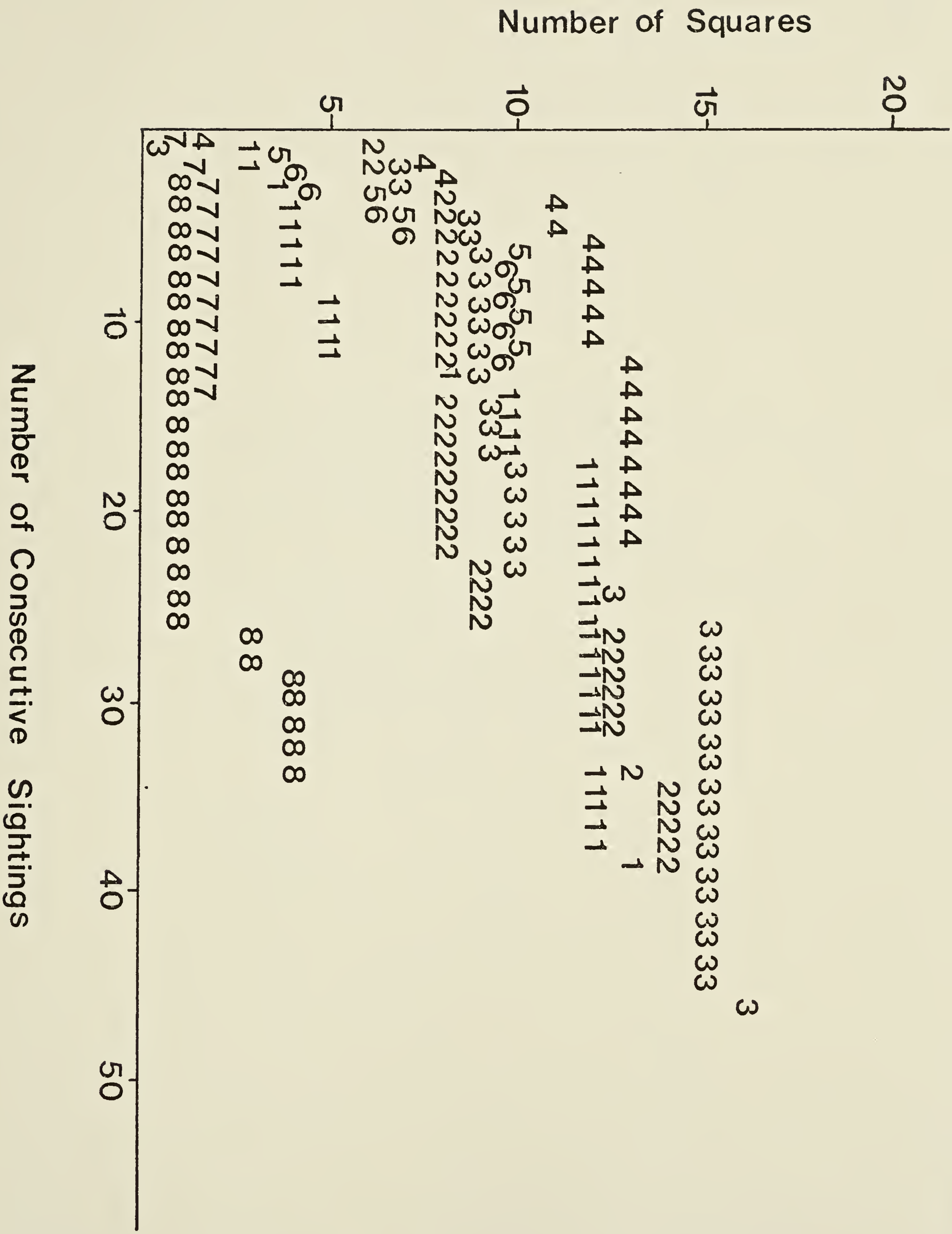
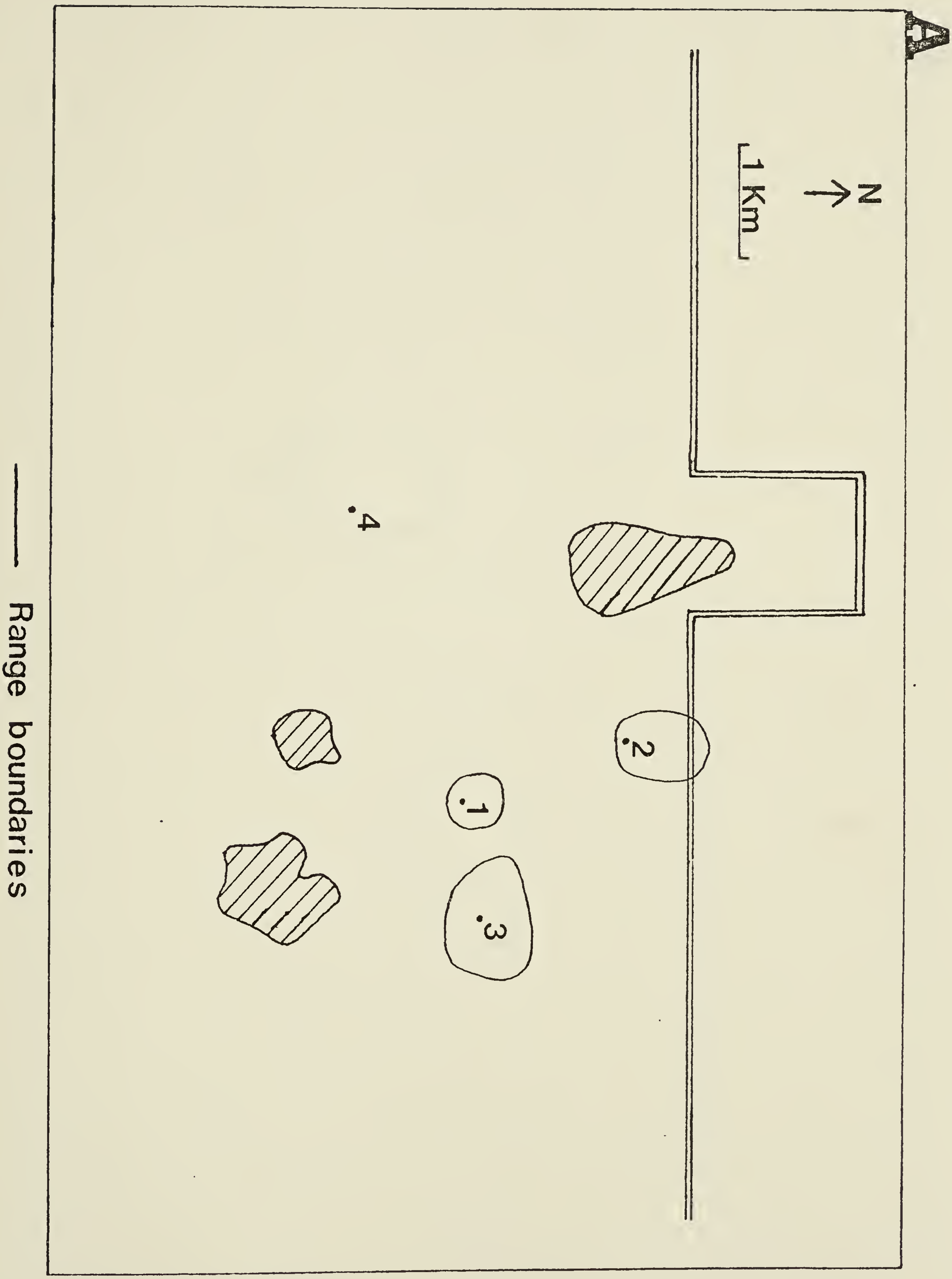
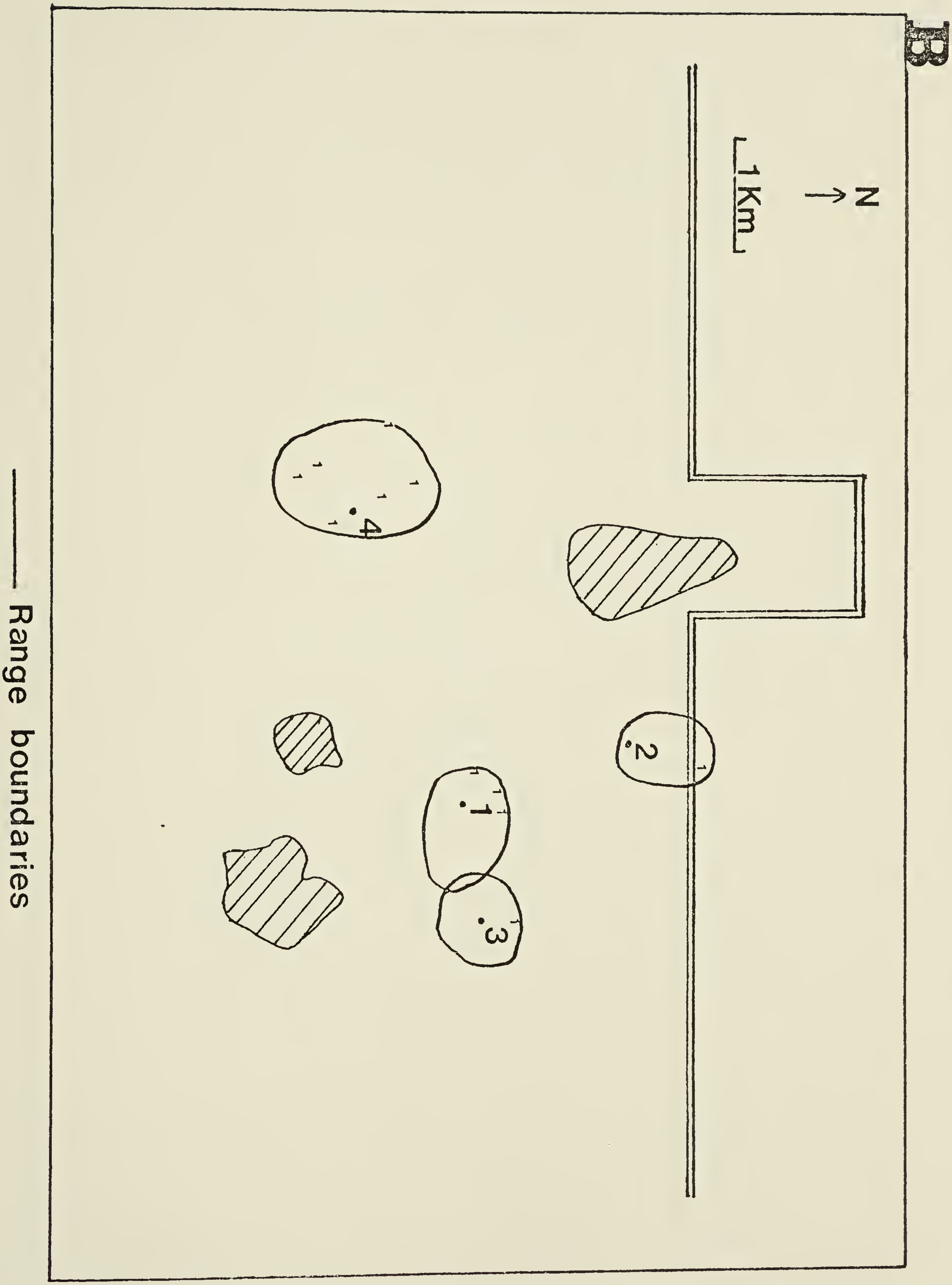
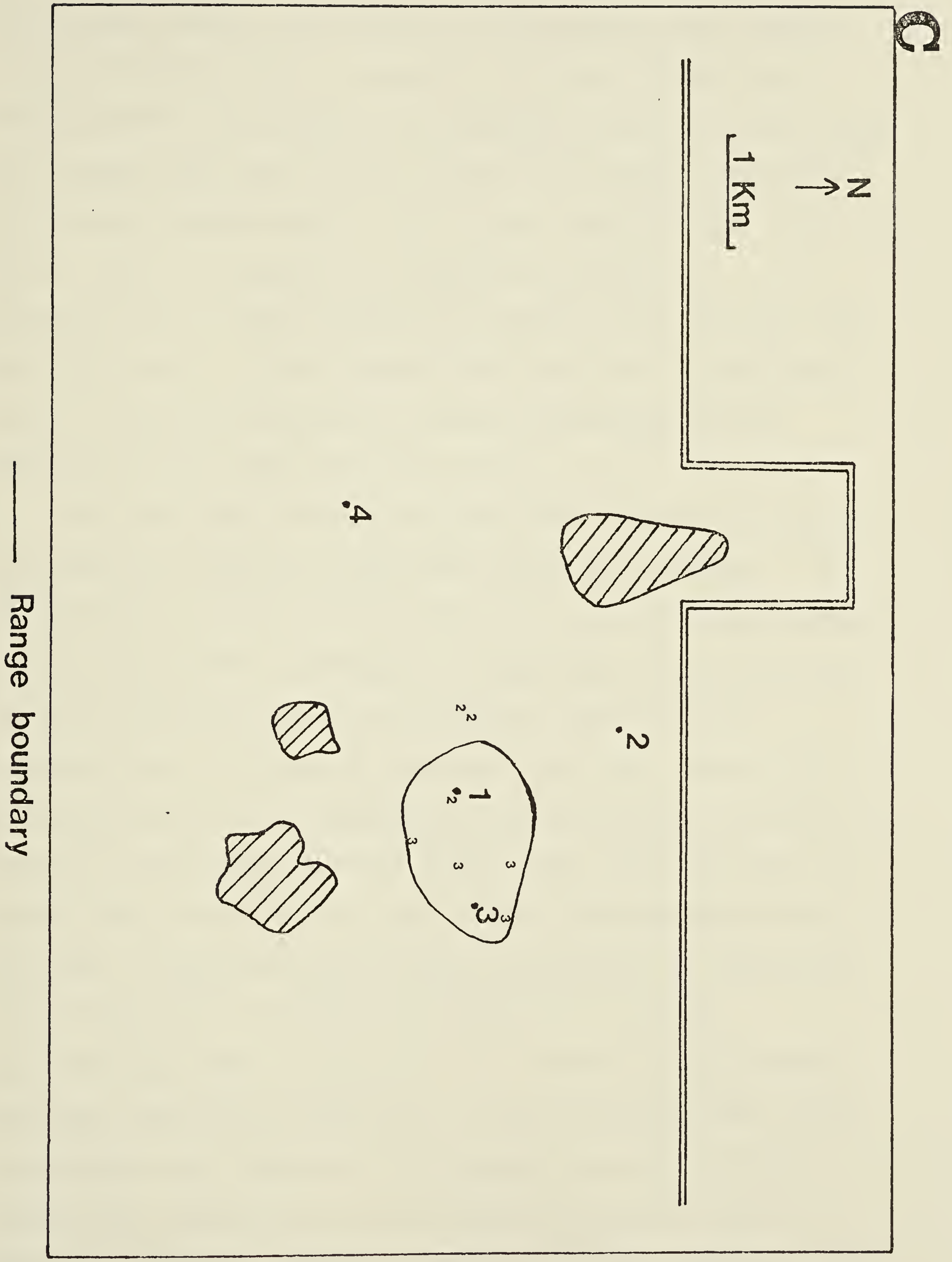

Number of Squares
Number of Consecutive Sightings

Figure 6. Ranges of territorial male sharp-tailed grouse away from Arenas BH, EBL, RBJ and WD during 1975 and 1976. 1 - Arena BH, 2 - Arena EBL, 3 - Arena WD, 4 - Arena RBJ. Refer to Figure 1.
A Ranges of males of Arenas BH, EBL and WD in summer, 1975.
B Ranges of males of all four arenas in spring, 1976. Sightings of wing-tagged males during winter are indicated by '1'.
C Range of males of Arena BH in autumn and winter, 1976. Sightings of the surviving males of Arenas EBL and WD with the males of Arena BH are indicated by '2' and '3', repectively.


A
N
1 Km
.4
.2
.1
.3
Range boundaries


B
N
1 Km
1
2
3
4
Range boundaries


C
N
1 Km
1
2
3
4
Range boundary

radius of one-half mile of the arena. Hamerstrom and Hamerstrom (1951) and Caldwell (1976) showed that lekking males remained within a radius of one mile of the arena during winter and ascribed the movements away from the arena to a search for food. Many of the long flights observed in this study originated from the arena after display. The males flew as a group in a sweeping arc over the 'hinterland' to land en masse at between about 500 and 900 m from the arena. These flights may have had an advertising effect in that conspecifics seeing them may have been attracted to the area near the arena.

The mean daily movements (with 95 % confidence limits) of territorial males of Arena RBJ (12.4±2.3) became significantly shorter after April 30 (4.4±1.8) (Mann-Whitney $U=2636.5$, $P<0.025$). Movements of two radio-tagged males of Arena WD for this period were similar (Mann-Whitney $U=258$; $P>0.05$) to those of males of Arena RBJ. Mean daily movements (with 95 % confidence limits) of males of Arena BH (9.5±1.1) were significantly longer than those of males on Arenas RBJ and WD for the same period (Mann-Whitney $U=298$; $P<0.025$). There were more visits by females to Arenas RBJ and WD (6.1 and 3.6 female-visits/display session, respectively) than to Arena BH (0.7 female-visits/display session) ($X^2=4.8$; $0.10>P>0.05$). Males of Arenas RBJ and WD restricted their movements to a smaller area around the arenas once females were present and copulations had occurred. However, males of Arena BH did not appear to have

this stimulus of large numbers of females on the arena and continued to make long daily movements.

The off-arena areas used by lekking males of Arenas EBL, RBJ and WD in summer and autumn of 1975 did not overlap (Fig. 6a). A shift in the area used by the males of Arena WD occurred during winter, 1976. Territorial males of Arena BH were seen to the north of the arena, in areas formerly used by males of Arena WD. In spring and summer, 1976, only slight overlap was determined (Fig. 6b). By autumn and winter, 1976, the males of Arena BH were using areas formerly used by males of Arena WD (Fig. 6c). The only known living male of the WD 'pack' did not display in autumn 1976 and was seen with territorial males of Arena BH on four occasions. This shift in areas used by males of these two arenas may have resulted from the increase in number of males and the resulting increase in level of activity on Arena BH. On four occasions, two during autumn 1975 and two during spring 1976, the males of Arena WD were seen to stop display. At these times display sounds from Arena BH were audible to the observer and probably also to the grouse on Arena WD. Perhaps, with an increase in intensity of display on Arena BH, the males of Arena WD shifted north and away from the area near Arena BH.

There was no display on Arenas EBL or WD during autumn and winter 1976. There was only one known survivor of each of these two groups of lekking males and both left their range around their respective arenas and were seen with the

territorial males of Arena BH. The male of Arena EBL attempted to display on Arena BH and was driven off. The decline in numbers of territorial males on these two arenas may be related to an increase in area around these arenas covered by aspen (Appendix 1).

The magnitude and direction of movements of newly-established territorial males showed a pattern of movement similar to that of established males of the same arena (Fig. 7). Mean daily movements (with 95% confidence limits) of these males were 10.2±3.8 squares and covered 240 ha. This similarity is to be expected as newly-established males were seen with established males on 13 occasions in autumn and winter of 1975 and 1976 vs six occasions alone.

Non-territorial males could be divided into two groups:

I - males that stayed near the capture arena

II - males that moved away from the capture arena.

Males of group I remained near the arena and consequently moved through fewer squares (108 ha) than did males in group II, which travelled over larger areas (554 ha; Fig. 8, Table 4). The slopes of the curves for males of group II were significantly steeper than slopes of curves for males in group I (Table 4). Slopes of the curves of males of group II were significantly steeper than slopes of established and newly-established territorial males in autumn and winter (Mann-Whitney U=0; P=0.036). Mean daily movements of males in group I were significantly less than those of males of group II (Table 4). The pattern of association with

Figure 7. The relationship between the cumulative area used by newly-established territorial male sharp-tailed grouse and number of sightings off the arena during autumn and winter (cf with Fig. 5). Cumulative area used by established males of the same arenas is included for comparison. Grouse numbered 1 and 2 were the newly-established male and established male, respectively from Arena BH. Grouse numbered 3 and 4-6 were the newly-established male and established males, repectively, of Arena EBL.

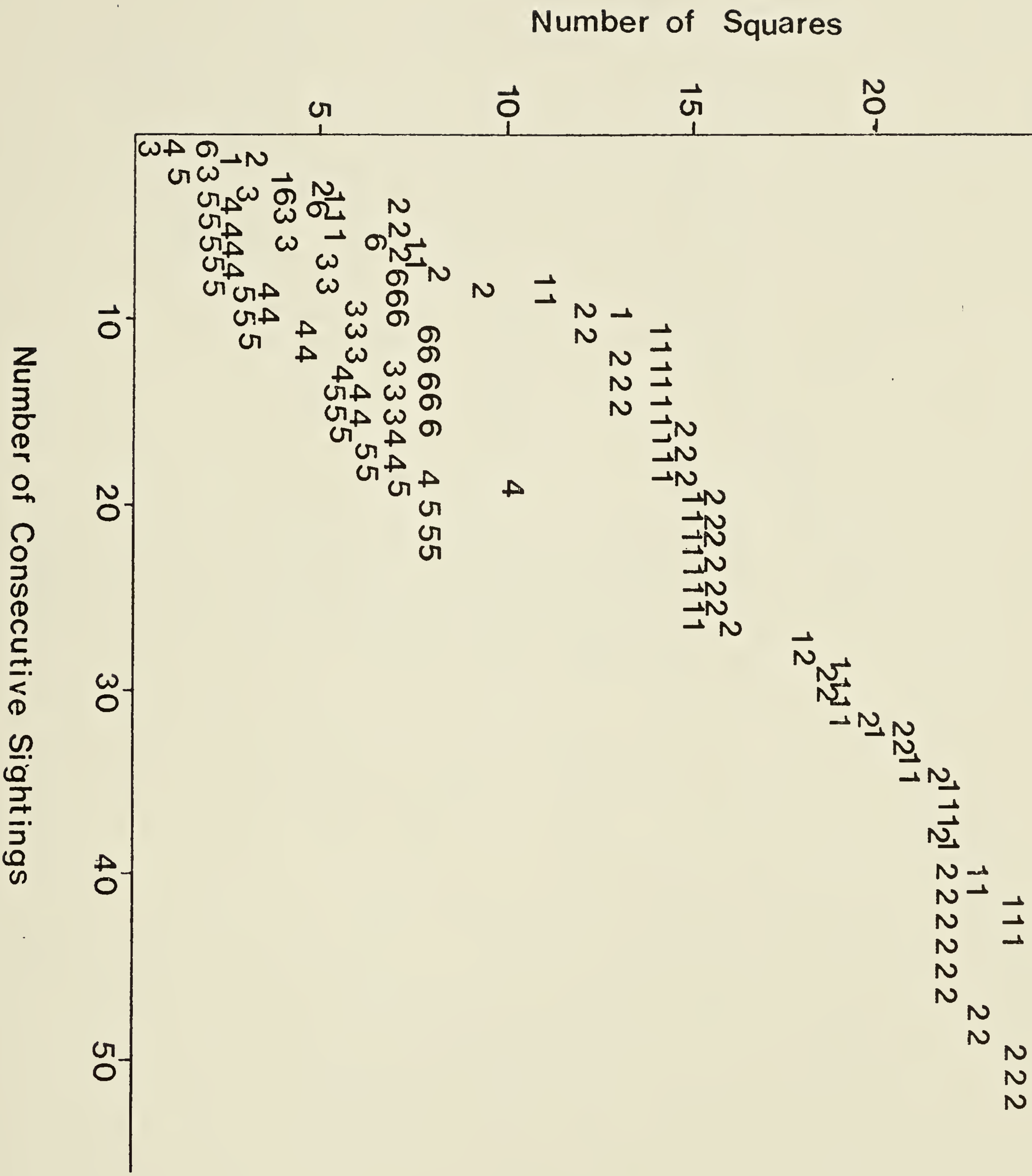

Number of Squares
5
10
15
20
25
Number of Consecutive Sightings
10
20
30
40
50

Figure 8. Comparison of total area used by non-territorial male sharp-tailed grouse during autumn and winter. Grouse numbered 1 and 2 were from group I and grouse numbered from 3-8 were from group II (cf with Fig. 5).

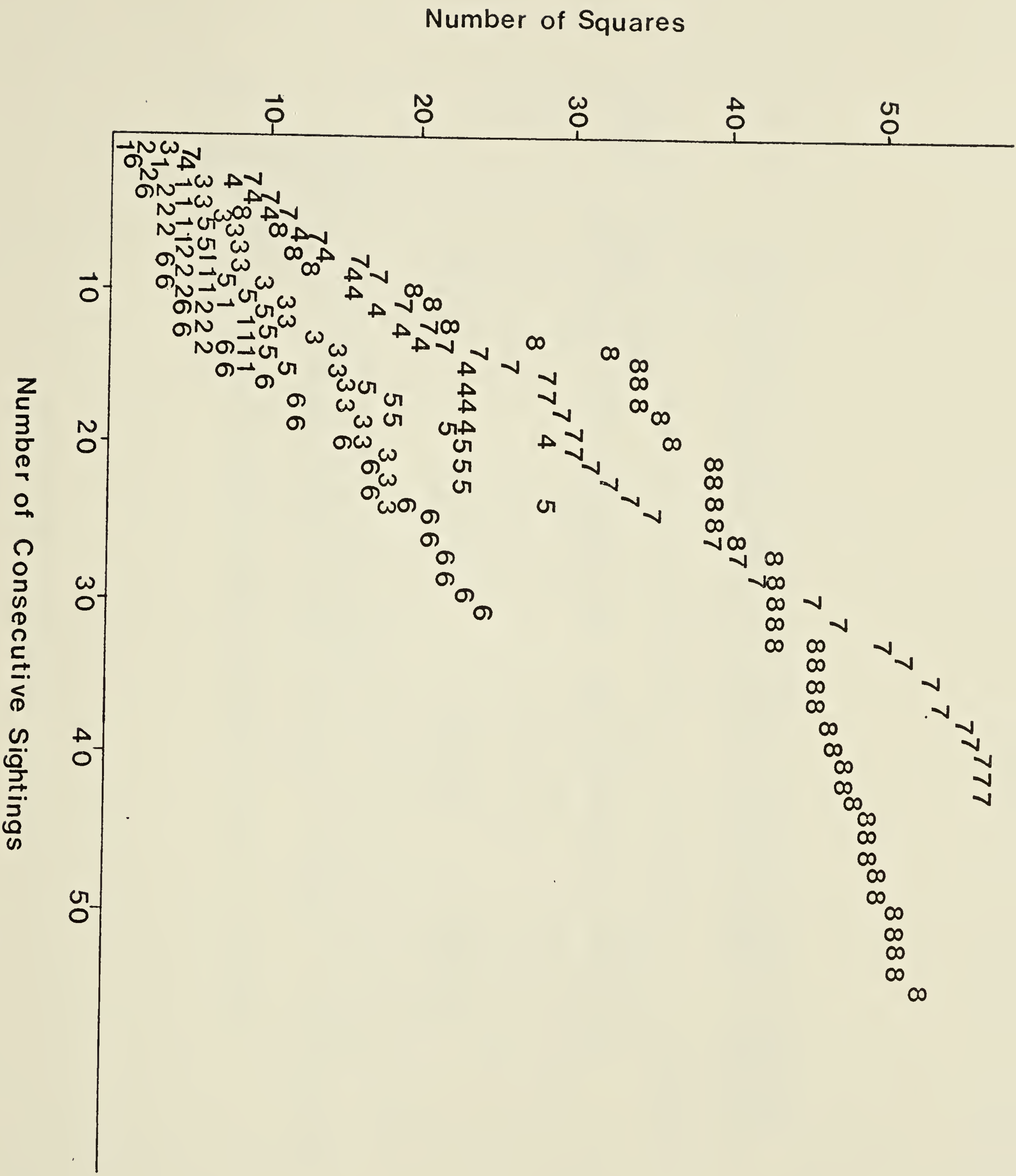

Number of Squares
Number of Consecutive Sightings
10
20
30
40
50

Table 4. Comparison of mean daily movement, distance of mean location from capture arena, amount of area used and slope of the area curve of non-territorial male sharp-tailed grouse of Groups I and II.

Group	Mean daily movement[1] (N)	Distance[2] (N)	Total area used[3] (N)	Slope of curve[4] (N)
I	7.7 (26)	780 (2)	7±1.4 (2)	0.44±.02 (2)
II	11.7 (197)	1335 (6)	35±16.1 (6)	1.02±.24 (6)
	F=5.7; $P<0.05$	MW[5] U=3; P=0.21	MW U=0; P=0.036	MW U=0; P=0.036

1 Average number of 1-cm squares touched by a straight line drawn between consecutive daily locations.
2 Distance from capture arena to mean locations (average of grids of all sightings.
3 Total number of 5 cm squares used by a male.
4 Slope of the curve of area used by a male. Refer to methods.
5 Mann-Whitney test.

conspecifics was significantly different between males of groups I and II as a result of the differences in movement between these two groups (Table 5).

These two groups of males illustrated the two basic strategies of non-territorial males. Males of group I showed an affinity for the area around the capture arena and appear to have restricted their efforts to gain territory to this arena. These two males did not seem to be adversely affected by the transmitters as they flew well when flushed. These males were occasionally seen with territorial males off the arena (Table 5). It may be advantageous to remain close to an arena so as to be able to be present at display sessions during this period. As sounds of display are audible for 800 to 1000 m (Hamerstrom and Hamerstrom 1960; pers. obs.), it was possible for non-territorial males to respond to these sounds and come to the arena. On eight occassions during displays in winter I recorded these grouse flying to the arena an average of 7.4 minutes after start of display. With the sporadic occurrence of winter display, a non-territorial male could be present for all displays and continue its attempts to gain territory.

The second strategy of a non-territorial male was to move away from the arena where captured and move through other areas. These males of group II may have been seeking groups of lekking males. If they had just been looking for conspecifics, they would have probably stopped wandering and localized in the first area in which they encountered other

Table 5. Number of sightings of transmitter-tagged non-territorial male sharp-tailed grouse of Groups I and II with conspecifics.

Group	Number of Sightings				
	alone	with territorial males	with non-territorial males	with other conspecifics	Total
I	11	9	3	0	23
II	31	10	13	28	82

$G = 20.4$; $p < 0.001$

grouse. Instead, the non-territorial males continued to wander through new areas (Fig. 8). All males in group II became localized briefly in small areas then moved again. In three cases, the males returned to the area around the capture arena, BH. Two of these males were seen with males of Arena BH. The movement of the non-territorial males appeared to have been in random directions but the possibility exists that the males that moved back to the area around Arena BH were returning to an area with a known group of lekking males.

Robel et al. (1970) and Bowman and Robel (1977) have reported long movements of juvenile male greater prairie chicken during disperal in autumn. Caldwell (1976) also described long movements of juvenile male sharp-tailed grouse in autumn which he attributed to dispersal. In this study, I believe that the movements of males of group II represented dispersal movements and that these birds were searching for arenas on which to establish themselves.

Aggression observed between non-territorial males around arenas may have been a factor in determining which males stayed near one arena and which birds moved. Caldwell (1976) and Bowman and Robel (1977) have postulated that dispersal may have been a result of aggression between the juvenile males.

The rate of mortality of non-territorial males during dispersal is difficult tc determine. Caldwell (1976) stated that the rate of loss during winter for juvenile sharp-

tailed grouse was greater than that for adult males. However, he was not able to determine what portion of the loss was a result of mortality or of dispersal. Bowman and Robel (1977) stated that juvenile greater prairie chicken were almost twice as vulnerable to predation as were adults and that juvenile males were especially vulnerable during dispersal movements in autumn. Perhaps non-territorial males are more vulnerable when moving through unfamiliar habitat. The selectively-advantageous strategy may be to stay by one arena and become familiarized with that area. Males of group I could benefit from their association with territorial males. An aggressive non-territorial male could remain by one arena and avoid the risk of increased mortality assumed to be in effect when moving through unfamiliar habitat.

In summary, analysis of movements of territorial and newly-established territorial males showed that these males concentrated their movements in the area around the arena. Group ranges of males of adjacent arenas were usually discrete, although change in size and area of ranges of two arenas was observed. Two groups of non-territorial males could be distinguished on the basis of degree of affinity for the area near the capture arena. Males of group I stayed near the capture arena while males of group II moved from the capture arena and showed little degree of concentration in any area. It may have been selectively-advantageous for a non-territorial male to remain near the

capture arena.

The 'importance' of the non-territorial male.

The non-territorial males provide a necessary reservoir from which males can be recruited during the autumn and winter. Without continued replacement from this pool, the number of males in a group would decline through winter mortality (Table 2). The level of activity of an arena is related to the number of males displaying (Caldwell 1976). The presence of arenas is advertised, either by display sounds (Lumsden 1965), or possibly, by long flights of territorial males out from the arenas. These displays may provide a stimulus that helps to keep non-territorial males in the vicinity of the arena. Brown (1970) reported that, on two arenas on which he recorded no autumn display, there were displaying birds, albeit only one male on each. In this study, there was no autumn or early winter display observed on either Arenas EBL or WD in 1976. In the spring of 1977, only one surviving territorial male of spring 1976 was present on Arena EBL and none on Arena WD. The effectiveness of single males in attracting females is probably less than that of arenas with several males. Thus, these two arenas were essentially ineffective.

Non-territorial males would be an essential component in the formation of new arenas. In years of 'good production' of young, the competition for available territories would probably be greater than in years of 'low production', assuming similar rates of mortality of

territorial males during summer. With more males attempting to fill vacancies, the number of non-territorial males wandering to different areas may be higher. These males may establish themselves on a new arena as a lekking group. Kruijt et al. (1972) reported the formation of an arena when a solitary displaying male black grouse was visited by females and other males. By the end of the display session, the new males had established territories around the original male. Peripheral male sharp-tailed grouse flew after females that flushed from the arena (pers. obs.). On two occasions display sounds were heard from the direction in which the male had flown. Perhaps non-territorial males could establish territories around a solitary displaying male in much the same manner as do black grouse.

The cumulative effect of non-territorial males through their recruitment and attempts to gain territory is summarized in Figure 9. The presence of non-territorial males on an arena increases the level of activity as the lekking males display to and chase them. In early spring peripheral males flew up to 40 m from the arena in pursuit of the non-territorial males. These flights may have had a similar advertising effect to that of flutter flights (Lumsden 1965). The increase in rate of display would enhance the advertisment of the arena and may be significant for the attraction of conspecifics to the arena.

Figure 9. Hypothetical effect of recruitment and the presence of non-territorial male sharp-tailed grouse on the level of activity at an arena and consequently its effectiveness in attracting females.

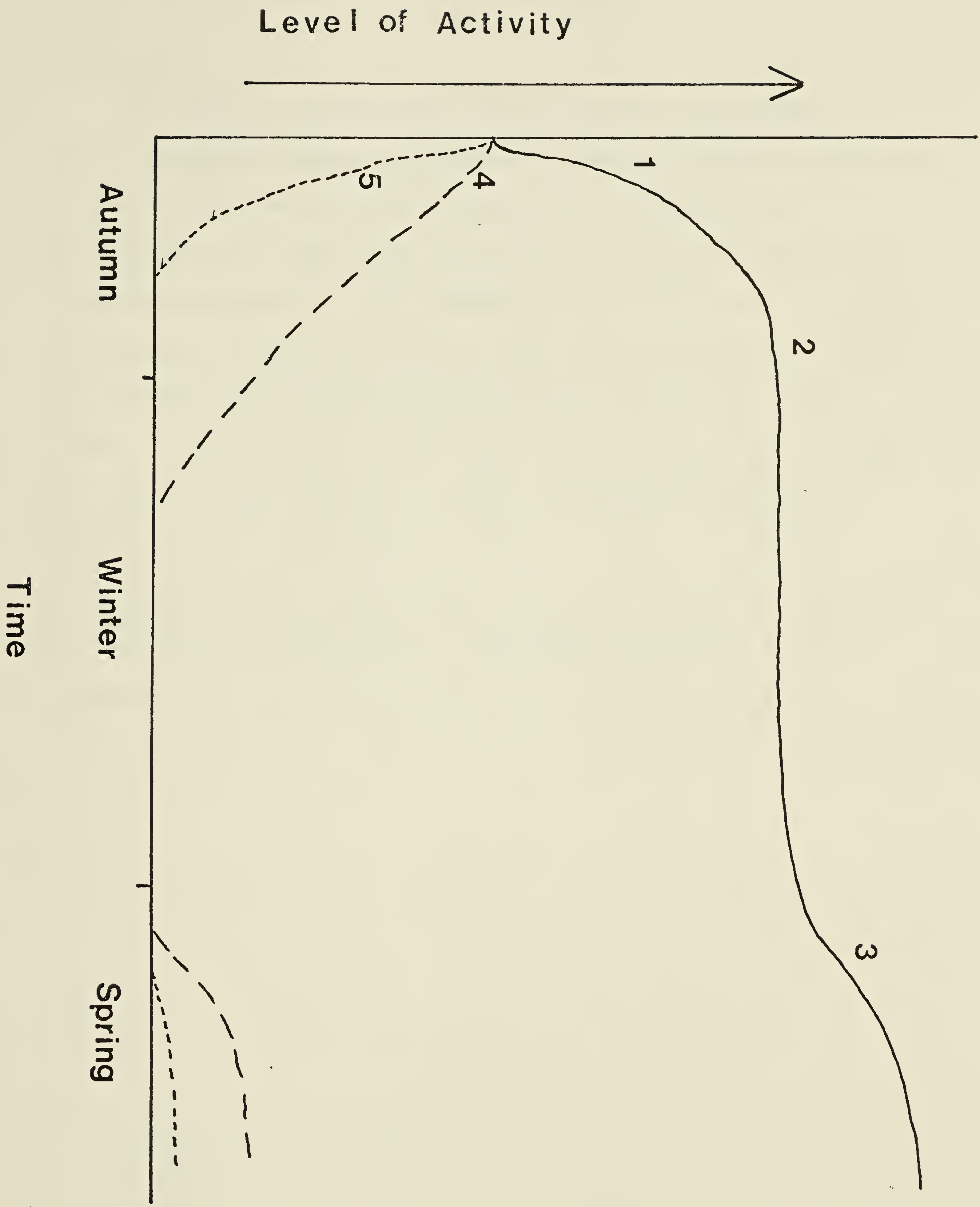
1 Recruitment of males in autumn produces an increase in the general level of display.

2 Recruitment and attempts to recruit during winter maintain the level of activity.

3 Chases of non-territorial males by peripheral territorial males increases the level of activity.

4 No recruitment. Display level declines as territorial males die. Little winter display and thus no stimulus for recruitment. Display in spring by survivors alone.

5 The situation on Arena EBL. Although no display was seen in autumn, 1976, there may have been some. There was no display during winter. Male G/G appeared alcne on Arena EBL in spring, 1977.



Level of Activity
Autumn
Winter
Spring
Time
1
2
3
4
5

CONCLUSIONS

The rate of recruitment of males into the lekking cohort of sharp-tailed grouse was greatest during autumn and winter. Males established themselves in peripheral positions on an arena and may have become established in a dominance hierarchy. The probability of adult males gaining territory in autumn is greater than that of juvenile males. Both established and newly-established territorial males showed a high degree of affinity for a reduced range around the arena. Non-territorial males differed in degree of affinity to the arena where captured, with some males staying and others moving from the area. I believe that the non-territorial males are an important component in the formation and maintenance of groups of lekking males.

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Appendix 1. Use of habitat by sharp-tailed grouse.

The vegetation at which sharp-tailed grouse were located was classified into one of seven types (1-grassland, 2-grassland-low shrub transition, 3-low shrub, 4-low shrub-tall shrub transition, 5-tall shrub, 6-trees, and 7-marsh). Since the study area was traversed at random and since dogs and telemetry gear were used to find grouse, these sightings gave a frequency distribution of occurrence of the grouse in the various types of vegetation. This distribution was compared with that of vegetative types taken from a large scale aerial photograph within the same area. Grid locations for the random points were derived from a table of randcm numbers; random points that fell outside the study area or in water were not used. This comparison showed that the grouse were not distributed randomly relative to available habitat types but that they showed preferences for certain vegetative types (Fig. 10).

The relative use of the seven vegetative types varied from season to season. Sharptails preferred the grassland and grassland-low shrub transition types throughout the year, especially in summer and autumn (Fig. 10). These two vegetative types were used for both food, in the form of buds, berries, flowers, and seeds present at various times of the year, and for roosting cover. Trees were heavily used in winter and spring, when grouse were observed feeding on aspen buds. Trees and tall shrub types also functioned as snow fences and the resultant drifts were used as sites

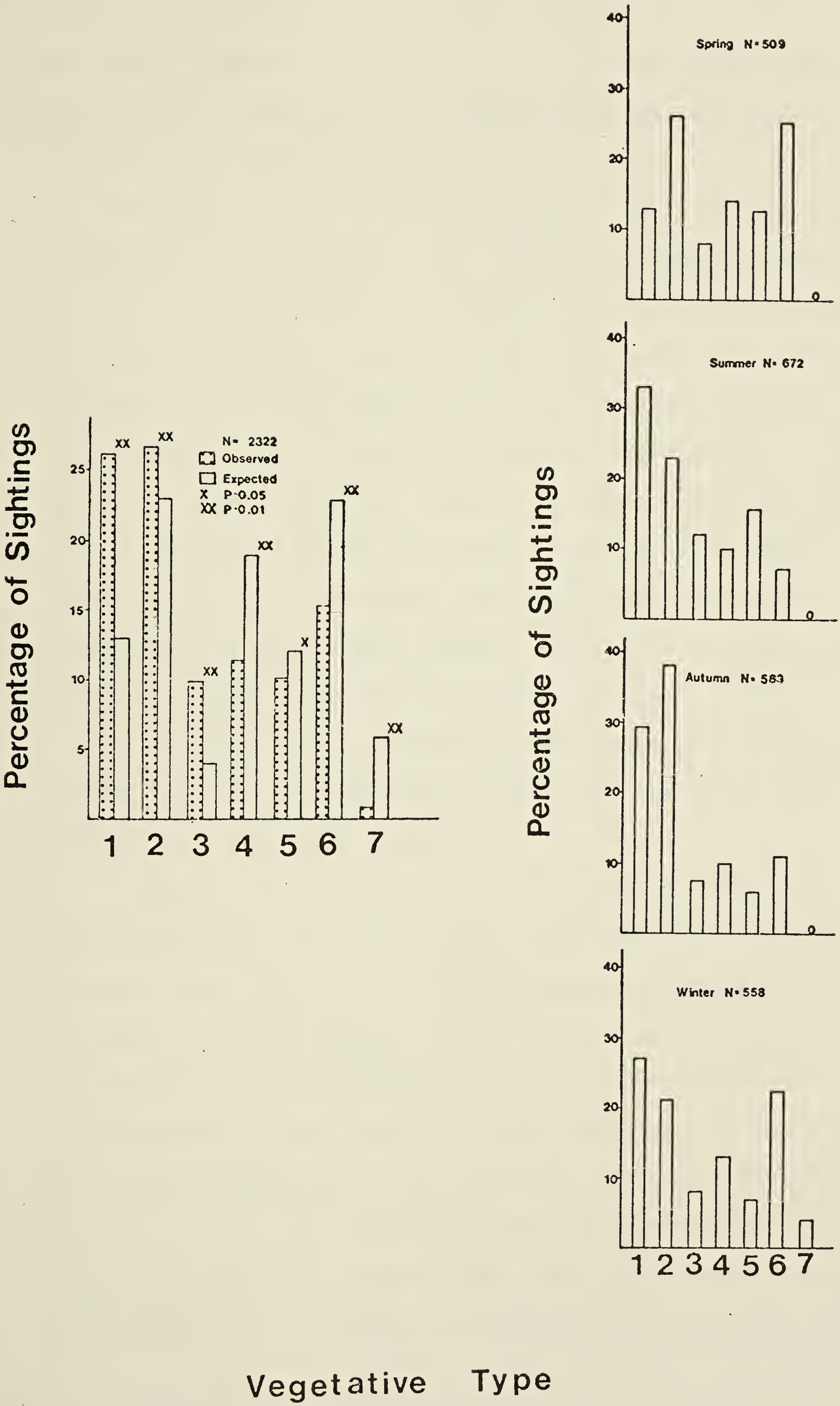
Figure 10. Use of vegetation by sharp-tailed grouse relative to its availability on the study area. Sightings of grouse are from 1975 and 1976. Expected values are based on randomly-selected points.

Spring - April 1 to June 15.

Summer - June 16 to August 31.

Autumn - September 1 to November 15.

Winter - November 16 to March 31.


Percentage of Sightings
N= 2322
Observed
Expected
X P-0.05
XX P-0.01
1 2 3 4 5 6 7
Spring N=509
Summer N= 672
Autumn N= 583
Winter N=558
Percentage of Sightings
1 2 3 4 5 6 7
Vegetative Type

for snow roosting. Marsh habitat was used almost soley in winter where Carex spp. and Salix spp. provided good roosting and feeding cover.

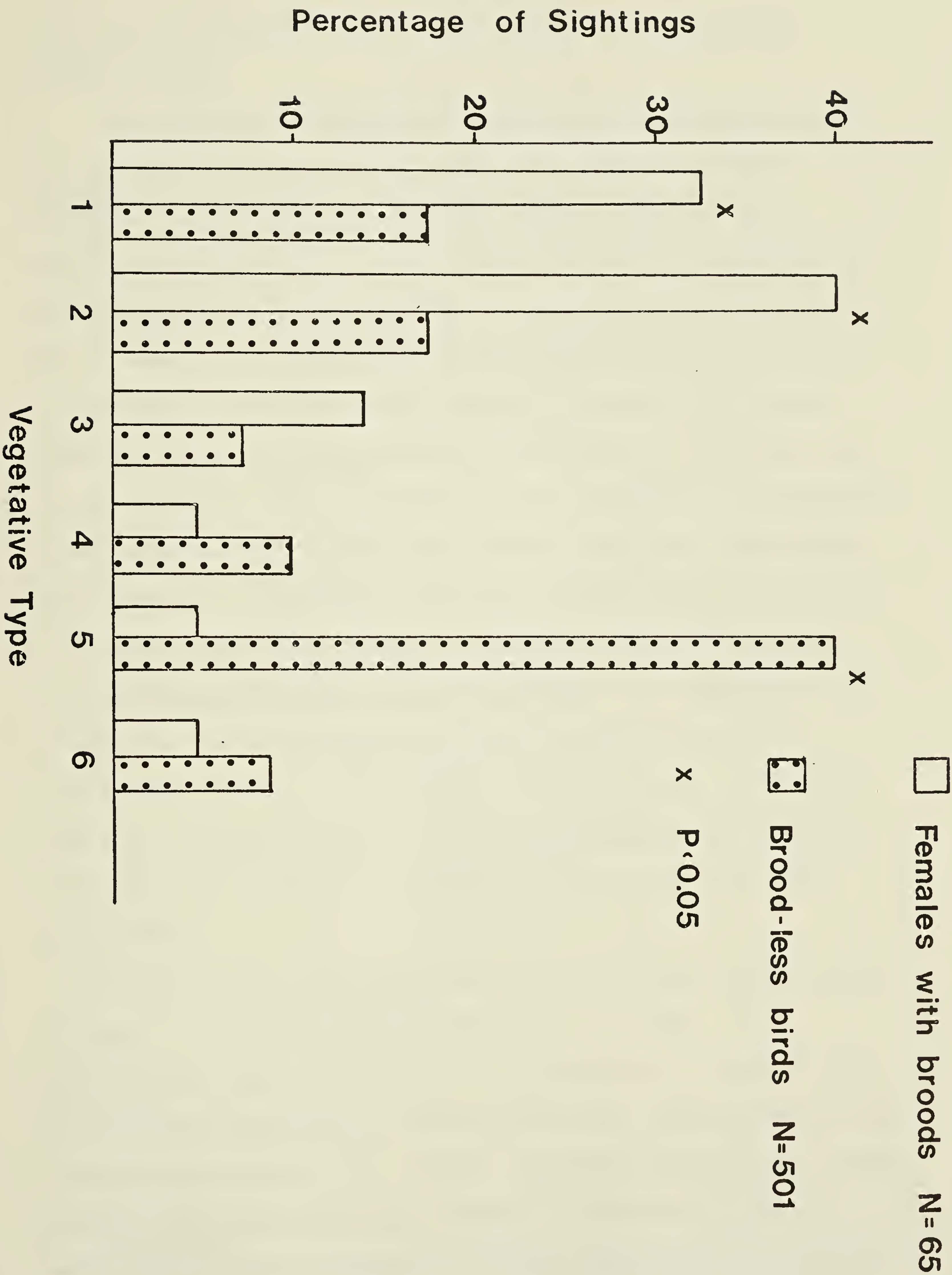
The use of the vegetative types in each season varied throughout the day (Fig. 11). In early morning throughout the year grouse preferred grassland-low shrub and grassland. In winter and early spring, grouse also used trees during morning. All three vegetative types provided food for the foraging grouse. During late morning and midday in all four seasons, grouse selected vegetative types which provided more cover; tall shrub and trees in spring and summer, low shrub-tall shrub transition and grassland- low shrub transition in autumn and winter. During late afternoon and evening, grouse were first foraging and then roosting and selected grassland-low shrub transition in all seasons; in winter some grouse also chose trees and low shrub-tall shrub transition vegetative types.

Females with broods selected mostly grassland and grassland-low shrub transition types (Fig. 12). Several authors have reported a similar preference (Hamerstrom 1963, Artmann 1970, and Pepper 1972). These two cover types provided food and roosting cover in a relatively drier microclimate as well as open space which may be important for evading predators. By contrast, males and females without broods selected tall shrub and grassland- low shrub vegetative types in summer (Fig. 12). The grouse could find both food and cover during the moult. At this time, the

Figure 11. Use of various vegetative types by sharp-tailed grouse throughout the day during the four seasons: spring-April 1 to June 15; summer-June 16 to August 31; autumn-September 1 to November 15; winter November 16 to March 31. During winter, the time periods were: dawn to 0800; 0801 to 1100; 1101 to 1400; 1400 to darkness.


Percentage of Sightings
dawn-0800
0801-1100
1101-1500
1501-dark
Spring
Summer
Autumn
Winter
N:33
N:48
N:331
N:259
N:215
N:158
N:98
N:38
N:206
N:187
N=124
Vegetative Type
1 2 3 4 5 6 7

Figure 12. Use of various vegetative types by female sharp-tailed grouse with broods and by brood-less birds (males and females) during the summers of 1975 and 1976.


Percentage of Sightings
10
20
30
40
1
2
3
4
5
6
Vegetative Type
Females with broods N=65
Brood-less birds N=501
x P<0.05

grouse were difficult to see and would not flush until forced to fly.

The relative frequencies and relative coverage of all plant species found in 522 plots were determined and combined to give the 'importance value' (IV) for each species during each of the seasons (Table 6). Grasses had the greatest IV in each season. Aspen was also important for grouse, even though the IV fluctuated from high values in spring and autumn to low values in summer and winter. However, in winter the percentage of aspen in the plots was almost equal to that in autumn. The contrasts in vegetative types selected by females with broods and males and brood-less females is apparent (Table 6). The IV and percentages of species typically found in grass and low shrub areas, such as _Symphoricarpos_, _Rosa_, _Artemisia_, and _Solidago_, are higher for sites of broods than for sites of males and brood-less females. In contrast, IV of species typically found in 'heavier cover', such as _Amelanchier_ and _Lathyrus_, were higher for sites of broodless grouse than for those with broods.

The effects of the weather variables were tested using multiple regression analysis (Nie _et al_. 1975). A hierarchical approach was used in analysing the effects of the weather variables as the effects were interrelated. The relationship between the weather variables cloud cover, wind speed, temperature and the degree of moisture of the vegetetation and the vegetative type selected by grouse was

Table 6. Importance values (IV) of all plant species found in the 522 plots put down at points where sharp-tailed grouse were seen.

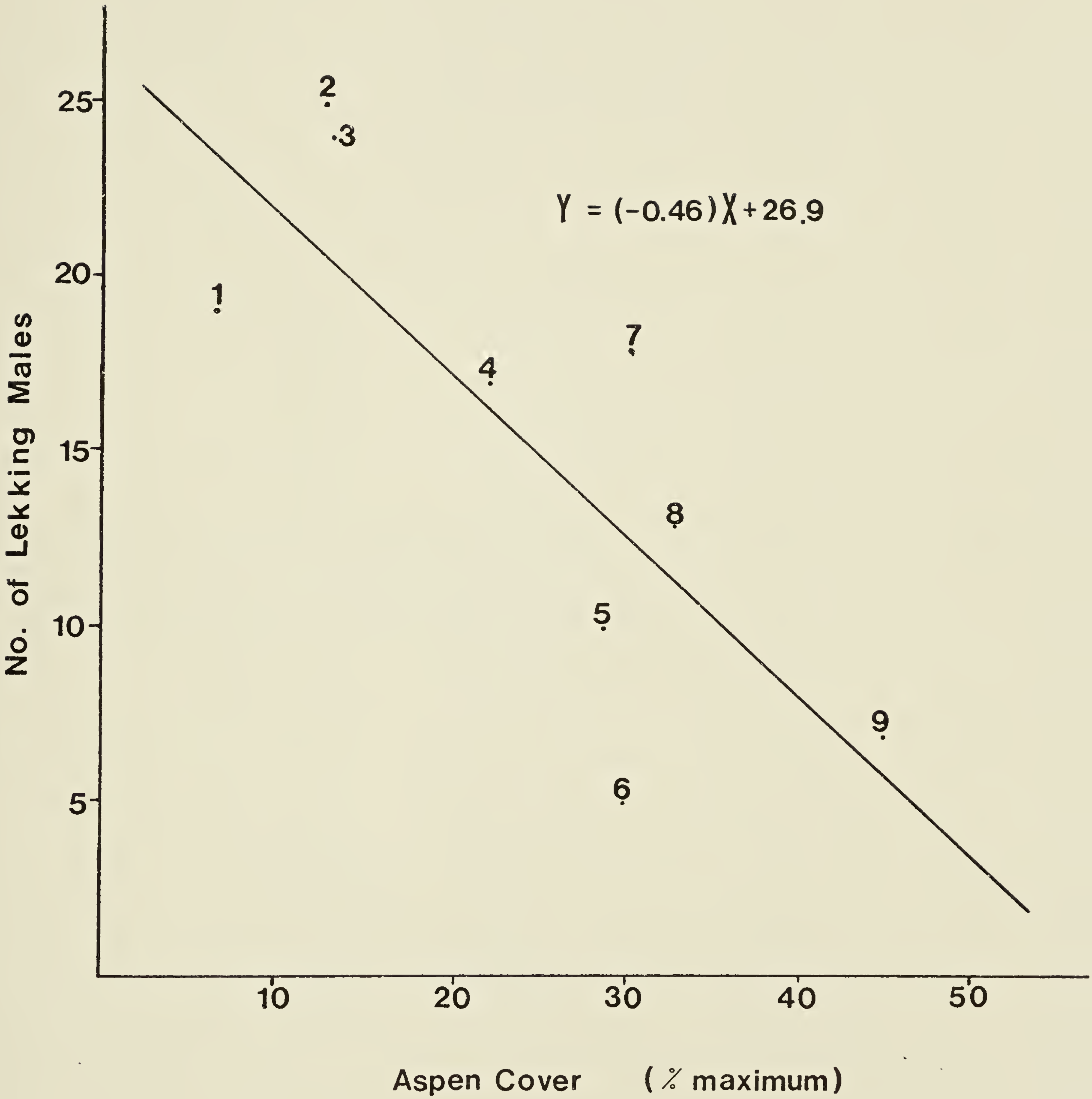
Species	Spring N=122	Summer N=158	Autumn N=119	Winter N=122	Brood N=56	Broodless N=102
Populus tremuloides	127.5 (16)[1]	76.1 (9)	110.8 (14)	75.3 (14)	47.9 (6)	91.5 (12)
Prunus	82.7 (11)	77.3 (9)	33.3 (4)	29.4 (5)	52.7 (7)	76.3 (10)
Rosa	53.3 (7)	41.2 (5)	43.5 (6)	40.7 (8)	50.3 (7)	36.3 (5)
Amelanchier	26.1 (3)	31.9 (4)	21.7 (3)	25.2 (5)	8.9 (1)	44.4 (6)
Symphoricarpos	18.3 (2)	24.2 (3)	19.5 (3)	34.8 (6)	41.7 (6)	14.5 (2)
Elaeagnus	16.7 (2)	29.1 (4)	20.0 (3)	23.9 (4)	36.6 (5)	25.0 (3)
Salix	8.2 (1)	3.0 (-)[2]	1.2 (-)	13.8 (3)	2.1 (-)	3.4 (-)
Arctostaphylos	61.1 (8)	29.1 (4)	45.9 (6)	20.6 (4)	2.1 (-)	29.7 (4)
Populus balsamifera	1.1 (-)	0.7 (-)	0	1.6 (-)	0	3.4 (-)
Lonicera	1.0 (-)	0	0	0	0	0
Shepherdia	0	0	0	1.1 (-)	0	0
Alnus	1.1 (-)	0	1.2 (-)	0	0	0
Gramineae	151.1 (20)	158.1 (19)	155.7 (20)	99.3 (18)	153.1 (20)	155.4 (20)
Carex	5.7 (-)	0	0	10.2 (2)	0	0
Artemisia	21.8 (3)	63.9 (8)	89.2 (12)	37.4 (7)	86.6 (11)	48.4 (6)
Aster	32.5 (4)	27.2 (3)	48.0 (6)	55.1 (10)	4.1 (-)	10.3 (1)
Galium	24.9 (3)	17.4 (2)	24.5 (3)	21.8 (4)	17.3 (2)	23.5 (3)
Achillea	13.4 (2)	31.4 (4)	18.6 (2)	6.9 (1)	32.7 (4)	27.6 (4)
Solidago	14.3 (2)	16.1 (2)	15.7 (2)	7.6 (1)	27.4 (4)	8.2 (1)
Chrysopsis	2.9 (-)	20.0 (2)	24.6 (3)	8.7 (2)	22.0 (3)	5.2 (-)
Lathyrus	14.6 (2)	12.0 (1)	10.8 (1)	7.6 (1)	3.9 (-)	17.5 (2)
Astragalus	1.9 (-)	8.2 (1)	0	2.9 (-)	11.4 (1)	5.8 (-)
Sonchus	1.0 (-)	7.2 (-)	6.9 (-)	0	11.0 (1)	3.4 (-)
Anemone	1.9 (-)	5.2 (-)	1.0 (-)	0	6.9 (-)	5.7 (-)
Thermopsis	4.8 (-)	21.7 (3)	1.0 (-)	0	25.0 (3)	19.8 (3)
Comandra	4.7 (-)	15.7 (2)	1.0 (-)	0	14.9 (2)	16.2 (2)
Vicia	13.1 (2)	14.0 (2)	6.9 (-)	1.0 (-)	8.9 (1)	16.5 (2)
Smilacina	3.8 (-)	6.6 (-)	4.9 (-)	3.8 (-)	7.1 (-)	8.0 (1)
Campanula	5.1 (-)	8.4 (1)	1.0 (-)	1.0 (-)	4.2 (-)	10.8 (1)
Gaillardia	0	3.0 (-)	2.0 (-)	0	2.1 (-)	3.4 (-)
Taraxacum	0	1.5 (-)	2.0 (-)	0	6.0 (-)	1.1 (-)
Cirsium	0	4.4 (-)	0	0	4.2 (-)	1.1 (-)
Potentilla	0	3.1 (-)	1.1 (-)	0	0	3.4 (-)
Epilobium	0	3.0 (-)	2.0 (-)	0	2.1 (-)	3.4 (-)
Zizia	0	2.2 (-)	0	0	0	3.4 (-)
Petalostemon	0	2.2 (-)	0	0	4.2 (-)	1.1 (-)
Linaria	0	0.7 (-)	0	0	2.1 (-)	0
Erigeron	0	1.5 (-)	0	0	0	2.3 (-)
Geum	0	1.5 (-)	0	0	2.1 (-)	1.7 (-)
Menthe	0	1.5 (-)	0	0	0	2.3 (-)
Antennaria	0	0.7 (-)	0	0	0	1.2 (-)
Medicago	0	0.7 (-)	0	0	1.0 (-)	0
Melilotus	0	0.7 (-)	0	0	0	1.2 (-)
Oxytropis	0	0.7 (-)	0	0	0	1.2 (-)
Equisetum	49.7 (6)	31.0 (3)	44.1 (6)	14.2 (2)	30.1 (4)	32.1 (4)
Moss-lichen-Selaginella	8.3 (-)	4.5 (-)	8.8 (-)	0	4.2 (-)	2.5 (-)

1 percentage of all IV for each season
2 less than 1 %

not strong as only 3.7 % of cover chosen by grouse could be explained as having been solely influenced by the weather. Obviously other factors, such as the absence or presence of conspecifics or familiarity with an area, were also critical in determining the choice of vegetation by a sharptail.

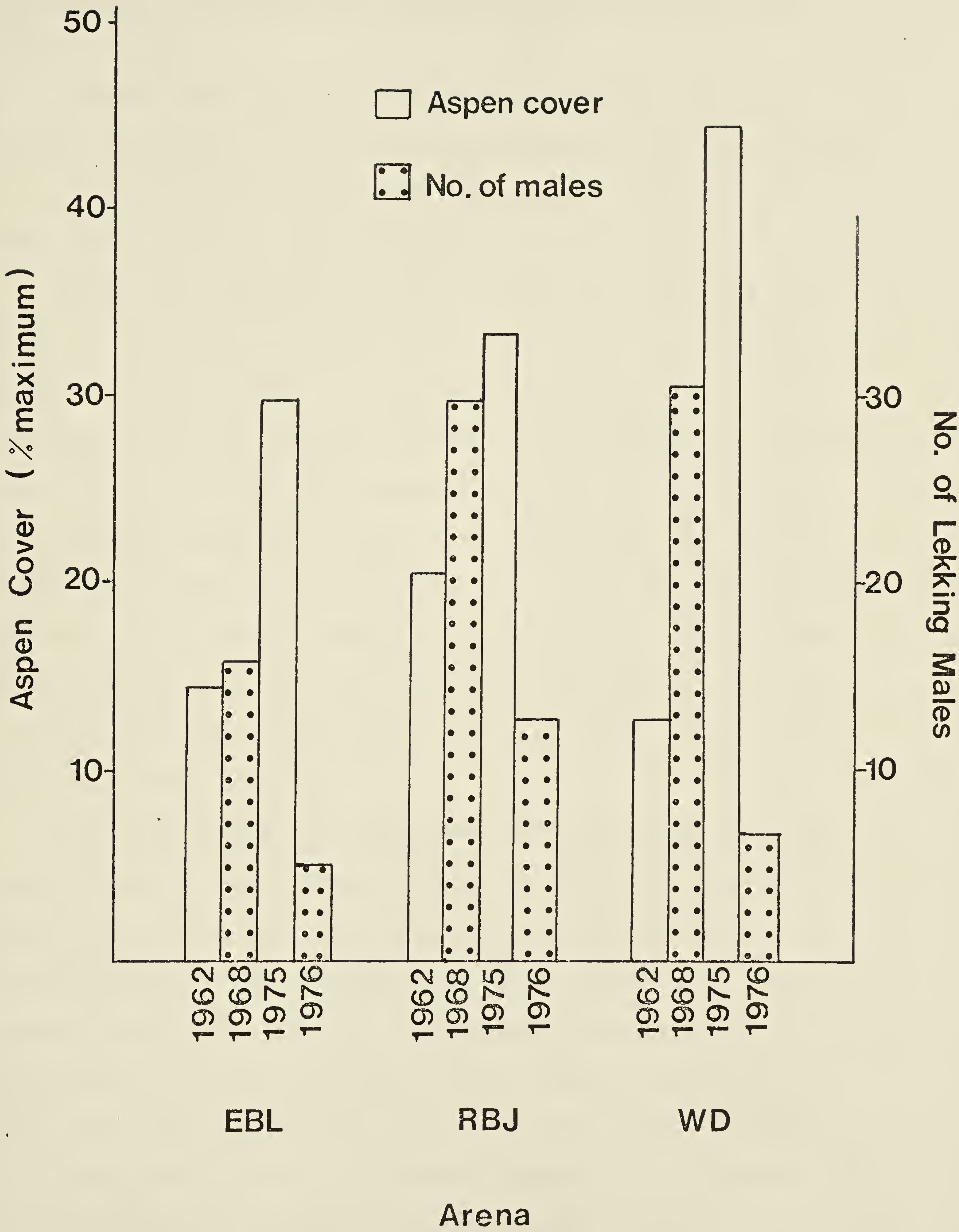
A mixture of grasses, low and tall shrubs and trees would seem to provide optimal conditions for the maintenance of sharp-tailed grouse in aspen parkland. The movement of succession towards a dominance of the habitat by aspen seemed to cause a decline in the population size of lekking males and by implication, of total population (Fig. 13). The areas around Arenas 2 and 3 (Fig. 13) have been burned annually in early springs whereas no program of regular burning has been conducted for at least 12 years around the remaining arenas (R. Duncan, pers. comm.). The area within 800 m of Arenas 6, 8 and 9 covered by aspen in 1962 was compared with the degree of aspen cover in 1975 (Fig. 14). There was a significant (Mann-Whitney U=0; P=0. 05) increase in cover. Associated with this increase in aspen coverage was a significant (Mann-Whitney U=0; P=0.05) decrease in the number of territorial males present on these three arenas (Fig. 14). The decline in numbers of lekking males may be an indication that this area is not as suitable for sharp-tailed grouse as it was in 1968.

Figure 13. Relationship between amount of aspen cover within a radius of 800 m of an arena and the number of lekking male sharp-tailed grouse on that arena. Aspen cover is expressed as a percentage of the maximum coverage possible. 1 - Arena 30, 2 - IO, 3 - Airport, 4 - SCL, 5 - BH, 6 - EBL, 7 - PIP, 8 - RBJ, 9 - WD.



No. of Lekking Males
25
20
15
10
5
1
2
3
4
5
6
7
8
9
Y = (-0.46)X + 26.9
10
20
30
40
50
Aspen Cover (% maximum)

Figure 14. Comparison of coverage of aspen within a radius of 800 m of Arenas EBL, RBJ and WD in 1962 and 1975 and comparison of the numbers of lekking male sharp-tailed grouse on these arenas in 1968 and 1976.


Aspen cover
No. of males
Aspen Cover (% maximum)
No. of Lekking Males
50
40
30
20
10
30
20
10
1962
1968
1975
1976
EBL
RBJ
WD
Arena

Appendix 2. Comparison of trapping methods used in this study.

Several techniques were used during this study to capture both sexes of sharp-tailed grouse of all ages (Table 7). I used several methods on the arena, including mist nets, walk-in traps, noose carpets and a drop net.

Nylon mist nets of 3.8 sq. cm mesh measuring 2.9 m in height and lengths varying from 17.6 to 22 m were strung between upright poles. Each pole consisted of two 1.8 m sections of 1.9 cm diameter conduit tubing which were fitted into a section of 2.5 cm diameter conduit 30 cm in length and secured by passing cotter pins through the 2.5 and 1.9 cm diameter tubes. The nets were set up on the arena in the afternoon prior to the morning display period. Grouse had to be flushed into the mist nets and often grouse that were not captured took a long time to return to the arena or did not return that morning.

The 'efficiency' of mist nets for this study was 0.05 grouse captured per attempt (Table 8.) The rate of injury of grouse when using mist nets was low relative to other methods but the rate of escape was high relative to other methods (Table 8). Grouse would often free themselves by struggling. On six occasions, grouse became entangled in mist nets while approaching the arena. On such occasions the other grouse became wary while watching the struggles of trapped grouse and would not come onto the arena.

Table 7. Number of sharp-tailed grouse captured by various methods in 1975 and 1976. Recaptures are included for a total of 222 grouse.

Time	Sex	Trapping Method					
		walk in trap	mist net	noose carpet	drop net	hand net	
1975							
Spring[1]	M	6	26		22		
	F		4				
Summer[2]	?[3]					12	
Autumn[4]	M	2	3		23		
1976							
Spring[5]	M		2	17	50		
	F				18		
Summer	F					1	
	?					14	
Autumn	M	1		2	13		
	F	3			3		
Total[6]		12 (6)	35 (17)	19 (9)	129 (60)	27 (8)	222

1. Spring - April 27 to June 15.
2. Summer - June 1 to August 31.
3. Juveniles--too young to determine sex.
4. Autumn - September 1 to November 15.
5. Spring - March 22 to June 15.
6. Percentage of grouse captured by each method indicated in brackets.

Table 8. Comparison of efficiency, rates of escape and injury, and deployment time of four trapping technique.

Technique	Number of times used	Number[1] of grouse caught	Number of grouse escaped (%)	Number of grouse injured (%)	Deployment time		Efficiency[2]
					Time (min)	No. people	
Drop net	35	130	1 (0.8)	4 (3.4)	40	2	0.05
Noose carpet	33	21	2 (9.5)	1 (5.3)	2	1	0.27
Mist net	39	42	7 (16.7)	1 (2.9)	10	2	0.05
Walk·in trap	44	16	4 (25)	0	15	1	0.05

1. Includes all recaptures.
2. Efficiency = (no caught − (no. escaped + no. injured))/ (no. of times that the method was used x the time required for deployment x no. of experienced people required for deployment).

The walk-in traps used were of the basic design presented by Rippin (1970) but were modified by covering the top with 0.3 cm thick plywood and attaching pieces of 8 oz weight green canvas to the sides. The traps were also made smaller for easier transport and handling. The traps were 1.4 m square and 0.5 m in height. The sides of the trap were covered with 1.3 cm diameter wire mesh. They were deployed in a triangle and connected by three funnel doors (Rippin 1970). A catch box, measuring 0.7 m in length by 0.5 m in width and 0.5 m in height, was placed against each trap.

During trapping efforts the canvas was rolled up, so that grouse could see through the trap. Once grouse had entered the trap, all canvas was lowered except that attached to the catch box. Grouse ran towards the light and thus into the catch box. The observer lowered a sliding door and confined the grouse to the catch box. The grouse was then removed through a hinged door in the top of the box.

In autumn, 1976, traps of Rippin's design (1970) were deployed on the edges of arenas. Wire of 2.54 cm in diameter, 0.7 m in height and lengths varying from 30 to 50 m were erected in a fan shaped pattern from each funnel door. Grouse walking onto the arena would be directed towards the trap entrance.

The efficiency of walk-in traps was equal to that mist nets and drop nets and lower than that of noose carpets.

The covered traps made removal of the trapped grouse easy but grouse seemed wary of entering the darkened interiors of the traps. The efficiency of the traps would have been greater had the larger walk-in traps of Rippin's design been used throughout the study. Larger traps covered more area on the arena and increased the probability of a grouse walking along the side and into the door. Once in the trap, grouse were continually trying to escape and would push against the wire mesh or try and fly through the roof. These attempts to escape usually resulted in minor scrapes of the beaks and wings.

Noose carpets (Anderson and Hamerstrom 1967) with nooses made of 20, 30, and 40 lb monofilament fishing line were used to capture territorial males. The nooses were tied to a carpet of mesh wire of a diameter of 2.54 cm so that the nooses were perpendicular to the carpet. Each carpet was attached to a weight by rope of lengths varying from four to six m. The rope allowed the grouse to drag the carpet and thus avoid breaking nooses (Anderson and Hamerstrom 1967). The dimensions of the carpet varied from 20 to 40 cm in length and 10 to 20 cm in width. The best dimensions relative to ease of handling and construction were 30 cm by 15 cm.

The carpets were most effective when activity of territorial males was great, such as when females were on the arena or when territorial males were chasing non-territorial males. Placement of noose carpets along

territorial boundaries increased the probability of capturing a territorial male.

The efficiency of noose carpets was greater than five times as efficient as any other technique (Table 7) while rates of escape and injury were low relative to the other methods.

The drop net was erected over an arena during the afternoon in preparation for the following morning's display. It consisted of a 10 m by 13 m rope net with a 3.75 sq cm mesh which was suspended at least 40 cm above the arena by four, 4-m poles. Each pole was anchored with a base plate and steadied with twc guy wires, The poles were erected so that once the net had been dropped, the poles fell away from the net. Each corner of the net was attached by a short piece of thin hemp rope to a winch cable mounted on the 4-m pole. The net was raised into place by winching up the four corners. An electrical blasting cap was taped to each rope and then connected to an electrical cable. A 12-volt battery was used to fire the four caps simultaneously. The net would then fall onto the grouse. All grouse were removed from underneath the net as quickly as possible.

Sharp-tailed grouse readily adjusted to the presence of the net and would crawl under the net if the net was almost on the ground. Grouse often perched on the net.

In cold weather, the firing cable would become brittle and snap. Also, the battery had to be kept warm to prevent

a failure. High winds disturbed the fall of the net by displacing it to one side.

The efficiency of the drop net was equal to that of mist nets and walk-in traps; rate of escape was relatively low but injury rate relatively high (Table 7). The efficiency rate may have been higher had the drop net not been used selectively to capture certain males. Of the four grouse seriously injured, one male was struck by a falling pole and killed. Two females suffered severe dislocations of the tarsometatarsl- tibiotarsal joint as a result of their entanglement in the net and attempts to free themselves. One male crawled under a net which was on the ground when one of the poles fell. This male became entangled and choked during its struggles.

Each method had advantages and disadvantages. The drop net, although capturing relatively large numbers of birds for each attempt, required considerable equipment, time and two experienced people to set it up. It is an effective method for capturing males on arenas where boundaries of territorial males are not known. Walk-in traps were reasonably effective on the edge of arenas as grouse were funneled into the traps as they walked onto the arena. These traps are also useful for trapping territorial males on the arena. Mist nets are light, portable and relatively easy to erect on an arena. However, they are not selective and grouse can be prematurely flushed by the inadvertent capture of one grouse. The noose carpets were the simplest

of the traps to place in position and to maintain. A knowledge of the locations of territorial boundaries is needed for greatest efficiency.

I attempted in both summers to capture chicks off the arenas. Success was low (Table 6) with captures by net or by hand. Once chicks began to fly, observers had poor success chasing and catching them. Chicks would fly and outdistance pursuers. Attempts to track chicks with dogs proved unsuccessful as chicks would run immediately after landing. Attempts to flush chicks into a hand-held mist net were partially successful. The hen and chicks would crouch when pointed by a dog. The net was set up then the chicks were flushed into the net. Chicks invariably flew towards the nearest bush, so nets were placed at right angles to the suspected path of flight. The drawback to the use of the mist net was the tendency of the net to catch on vegetation, poles and trappers. Once chicks were 8 to 9 weeks of age, they usually avoided the net with ease. The method of flushing chicks into a net did work but perhaps a cotton net would have been more practical than the nylon net.

Appendix 3. Reactions of territorial males associated with Arenas EBL, RBJ and WD to a playback of calls recorded on Arena WD.

Silvy and Robel (1967) used recordings of display calls of greater prairie chicken to recall lekking males to the arena. I used a playback of display sounds at three arenas in an attempt to stimulate rapid return of lekking males to the arena after they had flushed. The recordings used in this study were made on Arena WD during morning display on May 14, 1975 and contained "coos", "gobbles", "cork" notes and dancing sounds (Lumsden 1965). After the territorial males had flushed, the recordings were played for five minutes on a Sony cassette recorder with the volume control on maximum for broadcast of the sounds. The reactions of any males visible were recorded.

The reactions of lekking males of Arenas EBL and RBJ differed from reactions of males of Arena WD (Table 9). The males of Arena WD returned rapidly and began to display in response to the recordings whereas lekking males of Arenas EBL and RBJ did not return to display. Two territorial males of Arena EBL returned to the edge of the arena and stood in the "alert" posture (Lumsden 1965) before leaving once more.

Kermott and Oring (1975) reported that recordings of display sounds and calls of territorial males on one arena when played back to territorial males of another arena elicited display. The second group of males were on

Table 9. Reactions of territorial male sharp-tailed grouse to a playback of sounds of males recorded during their display at Arena WD.

Arena	Test No.	Position of males	Reactions of males
EBL	1	on edge of arena	no display
	2	on edge of arena	no display
	3	within 50 m of arena	two males walked to edge of arena- in 'alert' porture
RBJ	1	within 75 m of arena	no return
	2	within 75 m of arena	no return
WD	1	on edge of arena	return and display
	2	within 50 m of	return and display

territory and actively displaying just prior to the playback whereas the males tested in this study were only nearby. Territorial males of Arena WD may have been able to recognize calls of their neighbours whereas territorial males of the other two arenas could not recognize the calls and did not respond with display.

Significance of the calls, especially the "gobble" call, must be tested with playback experiments carried out under rigorous experimental conditions.

Appendix 4. Accuracy of telemetry system used in this study.

The accuracy of telemetry systems has been discussed by several authors. Slade et al. (1965) reported that errors increased as distance of the transmitters from the tower increased. Marshall (1963) and Slade et al. (1965) both mentioned the effects of thick clumps of vegetation and irregularities of topography on the directionability of the signal. Heezer and Tester (1967) introduced the concept of the "error polygon", based on a combination of location of the transmitter in relation to the tower and the "angular error". Incorrect interpretation of the signal by observers was described by both Slade et al. (1965) and Heezen and Tester (1967). Heezen and Tester (1967) stated that observer errors were no greater than 0.3° and 0.5° with good signals on calm and windy days, respectively.

In this study, the towers were placed on hills throughout the study area to try and overcome the problems of vegetation and topography. Distances between towers varied from 584 to 1280 m. As slippage of the compass dial was possible, alignment of the dial with true north was checked weekly with a compass. The alignment of the pointer with the yagi antenna was also checked weekly. Whenever the possibility of a grouse being directly between two towers occurred, a bearing from a third tower which was at right angles to the other two towers was taken. All observers using the telemetry gear in this study were instructed in

the proper identification of signals and their direction. Observer error was hard to determine but I believe it to have been slight.

Accuracy of the triangulation system was tested in June and December, 1976. Two observers took bearings from different towers to transmitters placed in the area. In the summer tests, the transmitter was held about 15 centimetres above ground level. The bearings were plotted on the aerial photograph of the area and positions determined by triangulation were compared with the actual locations (Table 10).

Accuracy was much less in late June than in December. As the leaves fell from trees and shrubs, the accuracy of this system improved.

Table 10. Mean error in determining positions of transmitter-tagged male sharp-tailed grouse by traingulation during summer and winter.

Season	Number of trials	Error (m) X (range)	Distance (m) transmitter to tower X (range)
Summer[1]	10	95.2 (40-120)	540.0 (160-888)
Winter[2]	10	28.3 (15-40)	563.2 (328-800)

1 June 16

2 December 27

Appendix 5. Two calls of sharp-tailed grouse heard but not previously described.

Thompson (1891) reported that sharp-tailed grouse gave "a soft clear whistle of three slurred notes, E A D" but did not state the situation in which the call was given. This call and two other calls similar in pitch and cadence but differing in tone were heard during this study.

Juvenile sharptails which were less that 6 weeks of age gave a whistle after a brood had been scattered. This whistle seemed to be a rally call as chicks would whistle in response to the whistles of an observer and walk towards the observer. Hart et al. (1952) reported a "distress call" but described it as a "peeping" sound.

Juveniles in autumn and winter were heard giving a 'raspy' call while one adult male was heard giving the clear whistle. Both calls were given in situations inwhich the grouse had been scattered and were regrouping. The clear whistle was given by an adult male which was the first of a group to return to the arena after having been disturbed.

On one occasion in winter, I had flushed a group of seven grouse, including one radio-tagged adult male. The grouse flushed as three subgroups, one of which landed in the tops of trees approximately 250 m from me. As I recorded this sighting, I heard the 'raspy' call from the subgroup that had flown south and could not see me. This call stopped when the grouse that could see me have a guttural clucking, similar to a call of females with broods

(Hart *et al* . 1952).

Perhaps the chick whistle, 'raspy' call and clear whistle have similar importance for sharp-tailed grouse. Sharptails are gregarious birds (Hamerstrom and Hamerstrom 1951; Caldwell 1976) and a rally call would be advantageous in communicating with the group. The similarity between chick whistle and 'raspy' and clear whistles, in pitch, cadence and in situations when the calls were heard, may indicate that these calls have the function of alerting conspecifics of a bird's presence and allowing groups to form or reform after they have been disturbed.